THE PHYLOGENY OF SOME MAYFLY GENERA

BY HERMAN T. SPIETH

(*Continued from Vol. XLI, page 86*)

PHYLOGENETIC RELATIONS OF GENERA

Super Family SIPHLONUROIDEA

Family *Siphlonuridæ*

Siphlonurus

This genus possesses the most primitive wing to be found within the order. In the fore wing (Fig. 3), R_3 is truly attached to R_2, and the R_3 triad has not been greatly modified. MP_1 is attached to MP_2 and this triad likewise has not been greatly changed from its primitive condition. CuA still shows distinctly a triadic method of forking on its distal end, and basally CuA and CuP meet as in the hypothetical primitive insect wing. Three anal veins are present. The interpolated veins are vigorous and attached basally.

The hind wing (Fig. 4) is large and Sc is only moderately arched; consequently the radial area is small. The radius and medians do not fuse but run into the base. The anterior median is triadically forked. There are no interpolated veins in the Cu area and three anals are found within the large anal area.

In contrast to the wings, the genitalia are specialized. In mature nymphs the forceps (Fig. 58) are 3-jointed, the styliger plate is flatly cone shaped and the penes can be distinguished as rod shaped organs. In the adult the styliger plate (Fig. 61) is extremely elongated and is longer than wide. The forceps which arise from the postero-lateral corners of the styliger plate are four-jointed, consisting of a short, heavy, trunk-like basal joint, a slender, slightly arced, long second segment, and two comparatively short, slender terminal members. The penes are distinctly divided into two separate organs which are accompanied by parameres and spurs. The penes, as well as the accessory organs, vary in shape among the different species.

The mouth parts are decidedly primitive in structure. The mandibles (Fig. 95) are of the generalized type. Both laciniae mobiles (Fig. 166) are similar. The maxillary palp (Fig. 118) is 3-jointed. The lacinia-galea (Fig. 118) is sturdy and has not been modified. It is straight, with a faint trace of the suture between the galea and the lacinia. The lacinial dentes are strong. The lacinial spurs are distributed along the inner surface. Setae are to be found on the terminal part of the galea and along the inner lacinial portion.

The labium (Fig. 143) likewise is primitive, having palps that are 3-jointed, while the mentum, submentum, and internal lobe are all small and match very closely the hypothetical, primitive type. Both glossae and paraglossae are distinct, not only in size and shape but also in method of attachment.

Gills are found on the first seven abdominal segments. The posterior five (Fig. 204) are large, foliaceous, single structures. They possess no filaments or other modifications, and merely represent an expanded, primitive gill. The tracheal method of ramification is distinctive. The two anterior pairs of gills (Figs. 198, 199) are similar to the others except that they are double instead of single. Each component of the double gills is much like one of the five posterior, single gills. According to Needham (1905) and McDunnough (1930), the nymph of *S. alternatus* is an exception in having all seven gills double.

To summarize, the wings strongly suggest that *Siphlonurus* is primitive. With the exception of the reduced secondaries and the accompanying changed shape of the primaries in the anal region the wings in this genus might be mistaken for those of the Permian Protereismidae. The data from the mouth parts (with the unmodified mandibles, lacinia-galea, and labium, the 3-jointed palps of both the labium and maxillae, and also the similar laciniae mobiles) parallel the wing findings. The 4-jointed forceps and the complicated penes indicate specialization. In regard to the shape of the joints and the styliger plate of the genitalia, *Siphlonurus* stands distinct from the remainder of the family.

The gills similarly show *Siphlonurus* to be distinct. The arrangement of double and single gills, and the shape and distribution of the trachea are peculiar to this genus.

Siphlonurus probably arose directly from the Protereismidae stock or from a stock that was closely related to the Protereismidae. While it has some peculiar specializations, it shows in the more conservative characters, especially the wings, a decided primitiveness, and occupies the lowest position in the phylogenetic scheme of the extant forms.

Family HEPTAGENIIDAE

Isonychia (*Chirotonetes*)

The wings of this genus are much like those of *Siphlonurus,* but display some specialization. In the fore wing (Fig. 10) the R_3 has broken away from R_2 and is now connected by a cross vein. The connection of MP_2 and MP_1 is greatly weakened and the CuA triad has been almost completely obscured. The anal area is smaller than in *Siphlonurus* and the interpolated veins are unattached basally. The hind wings (Fig. 11) are like those of *Siphlonurus* in so far as phylogenetic significance is concerned.

During the last nymphal instar the genital forceps (Fig. 57) are 2-jointed and are borne on an elongated, cone shaped styliger plate. Between the forceps two sharply pointed, posteriorly directed processes of the styliger plate are to be found. Between these processes the styliger plate is excavated.

In the adult state (Fig. 59) the forceps are 4-jointed. The styliger plate (Fig. 59) in *I. bicolor* wlk., and other closely related species is divided and consists of two narrow rectangular structures, from the terminal end of which arise the forceps. Basally, between these two structures, a posteriorly directed protuberance arises. In the case of *I. arida* Say and its close relatives the styliger plate is only slightly excavated. Doubtless this splitting of the styliger plate into two parts in the case of the bicolor complex represents a specialized condition. The penes (Fig. 59) in the case of the bicolor complex are simple, consisting of two posteriorly directed processes. In the arida complex, however, they are more complex having spines developed on a recurved protuberance that arises near the outer distal edge of the penes. (See McDunnough, Can. Ent. 63: 158.)

The mandibles (Fig. 91) are distinct, especially as to shape. The dentation is much like that of other generalized mandibles;

the outer right canine has three teeth, the inner right two teeth; and at the base on the posterior side a flange of the caine covers the lacinia mobilis. The two laciniae mobiles (Figs. 170, 171) are dissimilar. The maxillae (Fig. 119) show a distinct relationship to the remainder of the Heptageniidae. The palp is 2-jointed, with the terminal joint longer than the proximal joint. The lacinia-galea is expanded and, while not expanded so greatly as in the other Heptageniidae, the shape is the same. The lacinial dentes, and the arrangement of the hairs on the lacinia-galea and on the palps exhibit a primitive form which is probably close to the type from which the other more specialized Heptageniidae were derived.

The labium (Fig. 147) has 2-jointed palps. The paraglossae, the glossae, and the internal lobe are all distinctive in this genus.

Gills are to be found on the first seven abdominal segments. They are all alike except in size. They are compound, each gill consisting of an anterior, sub-oval, foliaceous lamella (Fig. 205) on the fore side of which runs an oblique ridge. The lamellae contain pinnately branching tracheae. The posterior part (Fig. 200) consists of a flattened fascicle of filaments. This type of gill (*i.e.,* one anterior lamella and a posterior flattened fascicle) is characteristic not only of *Isonychia* but also of its relatives the other Heptageniidae.

Isonychia, to sum up, has a venation and other wing characteristics such as shape, size of hind wings, etc., that indicate a fair amount of primitiveness. On the basis of the shape and number of the segments of the genital forceps, of the maxillae, and of the gills, *Isonychia* has been placed in the Heptageniidae. The shape of the penes, the condition of the styliger plate, the shape of the mandibles, and the labium, all indicate modifications that are peculiar to the genus itself and distinctly set it apart from all other existing forms.

Heptagenia, Ecdyonurus, Rhithrogena,* and *Epeorus.*

The remainder of the Heptageniidae, considered here, consist of a closely knit group of which there are six genera commonly

* Since this has been written, Traver has published two papers (Jour. Elisha Mitchell Sci. Soc., 48: 141–207; N. Y. Ent. Soc., 41: 105–125) in which he has designated the new genus *Stenonema,* which I find identical with the genus Ecdyonurus as defined here.

conceded to be present in North America, *i.e., Heptagenia, Ecdyonurus, Iron, Rhithrogena, Epeorus,* and *Cinygma.* All of these with the exception of *Heptagenia* were erected by Eaton who employed American material for *Iron,* but European material for the other four. *Heptagenia* was described by Walsh who used his *Heptagenia flavescens* as the genotype.

Eaton employed, as the primary means of identifying the various genera, the tarsal joints of the hind legs. Later Needham (1905) used the tarsal joints of the male fore tarsus, especially the first joint; McDunnough (1924) followed Needham. Eaton realized that the use of tarsal joints was beset with difficulties due to the shrinkage of the members and due to the fact that regenerated nymphal legs did not mature into normal organs. The use of the fore leg is encumbered with more difficulties because, in addition to the above mentioned ones, these members are very delicate and are usually the first part of the body to be lost. Furthermore, this system leaves no method for identifying females.

This group can never be thoroughly understood and a natural classification—one that will express the evolution of the group—can never be constructed, until the nymphal and adult stages have been connected for a large number of species, and until large series over wide-spread areas have been collected. Then by utilizing all nymphal and adult characters, a true and natural classification may be designed. At this time I do not have enough material, especially in the genera *Epeorus* and *Rhithrogena,* for a thorough and detailed discussion of the group. Consequently this discussion is restricted to pointing out a few of the evolutionary changes that the group has undergone. This discussion is based mainly upon nymphal material. *Iron* and *Cingyma,* of which the nymphs of the latter are unknown, are omitted.

The wings (Figs. 5, 6, 12, 13, 14) of all of these genera are uniform in so far as the primary venation is concerned. In the fore wings the R_3 has become detached from R_2 and is now connected to R_2 by cross veins. The R_3 triad has been modified so that R_{3b} appears as the direct prolongation of R_3 and thus R_{3a} is a distinct vein. MP_2 is distinctly attached to MP_1 well out on the wing so that the M triad is as primitive as that found in *Siphlonurus.*

The Cu_1 triad, which was found in the Protereismidae and *Siphlonurus,* has become completely obliterated. Two pairs of interpolated veins are to be found within the Cu area, these constituting the distinguishing marks of these genera. At their bases CuA and CuP bend forward so as to lie very close to M within the wing root. Three anals and two interpolated veins are present.

In the hind wings (Figs. 7, 14, 16) Sc is more strongly arched than in *Siphlonurus*; MA and R are fused out to the level of the costal projection; and MA gives rise to a triad. There is a pair of interpolated veins between CuA and CuP, except in the *Heptagenia maculipennis* complex where they are lacking. The anal area is greatly reduced with A_1 and IA_1 distinct and A_2 a short unattached vein.

Concerning the cross veins and the pigmentation of the veins there is a great amount of variability, as was indicated in the section on cross veins. This cross-venation apparently is not a valid criterion for the recognition of genera, although it may indicate the lines of evolution within each genus. This is shown by the genus *Ecdyonurus* which has three distinct modifications of cross venation. Thus the *E. tripunctata* complex has one group in which the cross veins are aggregated in the region of the bulla as far back as the costa (Fig. 6), and another (Fig. 12) in which there is no indication of aggregation. In the *E. interpunctata* complex there is an aggregation extending back to the R_2, and also a long, longitudinal black streak between the R_1 and R_2 in the region of the bulla (Fig. 5). In the *maculipennis* complex of the genus *Heptagenia* there are two types of cross venation, one with aggregation and one without it.

In the mature nymphs the genitalia (Figs. 50, 51, 52, 66, 67) are similar to that of *Isonychia* with the exception that the part of the styliger plate lying between the bases of the forceps consists of a hump shaped structure and is usually not deeply excavated as in *Isonychia.* In the adults, the forceps (Figs. 49, 53, 60, 62) which are much like those found in *Isonychia,* consist of a short somewhat conical joint, a long slender second joint, and two short slender terminal joints. These are constant throughout the group. The styliger plate (Figs. 49, 53, 60, 62) likewise is uniform throughout the group. The penes, however, are highly variable. In the genus *Ecdyonurus* two distinct types are to be found: one with L shaped penes (the *tripunctata* complex, Fig. 53), and the other with penes which are stub-like and slightly expanded at the tip (*interpunctata* complex, Fig. 60). In the genus *Heptagenia* the species of the *maculipennis* complex have peculiar penes which differ considerably from those of the other *Heptagenia* species. The reader is referred to the sketches of McDunnough for further information on the variability of the penes of the species of Heptageniidae.

The mandibles are quite constant in shape (Figs. 97, 98, 100, 101, 102) and the molar area is not highly variable. The incisors and laciniae mobiles, on the other hand, are quite variable. The lacinia mobili is present in some of the *Heptagenia* as a group of large setae (Fig. 185), and in *Ecdyonurus interpunctata* (Fig. 174) as a single hair; and it is lacking in all the rest. The inner incisors are reduced in *Ecdyonurus* and *Heptagenia* (Figs. 99, 101, 102), having one prong terminating in a sharp point, while the other retains its normal shape. In *Epeorus* they are greatly reduced but not sharply pointed (Fig. 100), while in *Rhithrogena* (Fig. 98) the inner incisors are almost lacking. With this reduction there has been an enlargement of the outer incisors. Generally speaking they are scoop-shaped and vary in size inversely to the inner members, being moderate in size in *Heptagenia* and very large in *Rhithrogena.*

The maxillae have 2-jointed palps. The terminal segment is long, expanded, and hairy, thus forming an efficient sweeping organ to brush food into the mouth (Figs. 120, 121, 124, 125, 128, 130). The maxillae of *Heptagenia* (Fig. 124) and *Ecdyonurus* (Figs. 125, 128, 130) are similar in size and shape, while those of *Rhithrogena* (Fig. 120), and *Epeorus* (Fig. 121) approach each other in appearance. In *Rhithrogena* the hairs of the terminal segment have become enormously enlarged with secondary, lateral processes which form a unilateral, comb-like organ (Fig. 120).

The lacinia-galea in *Heptagenia* and *Ecdyonurus* is a large, broadly expanded organ with a characteristic shape (Figs. 124, 125). The lacinial dentes are greatly reduced, and the lacinial spurs are fine. Along the straight edge of the lacinia, a closely set row of slender setae extend. Another row of widely spread setae is located more nearly on the median axis of the lacinia. On the end of the lacinia-galea there are a number of setae. In *Heptagenia* these have become enormously enlarged and secondarily branched at their inner, distal margins so as to form comb-like structures (Fig. 124). In *Ecdyonurus,* especially in the *tripunctata* complex (Fig. 130), this modification of the seta is only slightly indicated. In *Epeorus* (Fig. 121) and *Rhithrogena* (Fig. 120), the lacinia-galea is much stouter and terminally much narrower than in *Heptagenia.* Those of *Epeorus* are armed terminally with three massive teeth (Fig. 121), while the setae on the galea portion are reduced to a minimum. *Rhithrogena* (Fig. 120), with a lacinia-galea that compares with that of *Epeorus,* lacks the heavy tooth-like structure. It has galeal setae and lacinial dentes as in *Heptagenia.*

The labium (Figs. 142, 145, 146, 148, 149) is a rather uniform structure throughout the group and consists of a broadly expanded internal lobe with large flat paraglossae and finger-like glossae. The 2-jointed palps are enormous and flattened. The basal joint is pear-shaped and attached on one side to the internal lobe. The short, heavy, second joint bears on its inner surface an area that is densely covered with setae.

The gills are all of the same type as described for *Isonychia,* each gill consisting of an anterior foliaceous lamella that serves for both protection and respiration, and a posterior fasciculated member which is wholly respiratory in function. The shape of the anterior lamellae varies greatly. In *Epeorus* (Figs. 209, 210), whose species live in swift currents, the anterior lamellae are beset with an area of spines on their outer edge so that the gills can serve as grasping organs. Thus the nymphs are enabled to climb the face of a vertical stone wall or to maintain themselves in swift currents. When the anterior lamellae are being employed in this manner, the fasciculated posterior lamellae are so constructed that they extend out between the body of the animal and the inner basal part of the shield portion and thus are exposed to the wash of the water. In such nymphs, the posterior gill portions are small. *Rhithrogena* has the anterior parts of the first pair of gills greatly elongated so that the front edges of these come in contact with each other under the abdomen, but the outer edges of the anterior lamellae are not as greatly modified for prehensile organs as in *Epeorus*.

Ecdyonurus and *Heptagenia* both live in still or only moderately swift water, and the gills are not adapted for grasping and suction as in the above mentioned genera. Further, the posterior, fasciculated lamellae can retain their normal position behind the leaf-like anterior members and still be exposed for aeration. The posterior lamellae are large (Figs. 202, 207, 216) providing a large aerating organ for use in the quieter water in which they dwell. In the *Heptagenia* the seventh gill usually consists of both an anterior and posterior portion, but the posterior part may be lacking as in the *H. maculipennis* complex (Fig. 215). The genus *Ecdyonurus* has the posterior part of the seventh gill completely lacking and the anterior part has been reduced to a small structure shaped like an arrow-head (Figs. 203, 208). In the first six gills of the *E. tripunctata* complex, the anterior lamellae are elongate, quadrilateral structures (Fig. 201), while in the *E. interpunctata* complex the corresponding members are broadly obovate and terminate distally in a sharp point (Fig. 206).

From the above evidence, incomplete as it is, two distinct major lines of evolution can be distinguished. One is represented by *Heptagenia* and *Ecdyonurus* and the other by *Epeorus* and *Rhithrogena*.

Ecdyonurus, on the basis of wings, genitalia, gills, and maxillae, displays two lines of development. One is represented by the *tripunctata* and the other by the *interpunctata* complex. The latter appears to be more closely related to *Heptagenia* than is the former. The genus *Heptagenia* (when sufficient amounts of material have been studied) will doubtless show as divergent lines of development as *Ecdyonurus* does. The *maculipennis* complex will probably represent one of these lines.

On the basis of nymphal characters, *Epeorus* and *Rhithrogena* are all closely related. The maxillae, however, show *Epeorus* to be distinct, while *Rhithrogena* (although displaying distinct affinities) also shows a similarity to the more primitive species of *Heptagenia.* This group can not be profitably discussed until further data are available.

Family Baëtidae

The genera *Callibaëtis, Baëtis, Centroptilium, Cloëon,* and *Pseudocloëon* all have been derived from a common stock and still form a closely compact group. The most striking characteristic of these genera is the excessive reduction that the metathoracic wings have undergone. This reduction reaches its extreme development in *Cloëon* and *Pseudocloëon* where the hind wings are completely lacking. In the fore wing the cross venation has been greatly reduced and the basal attachments of MA_2 and MP_2 with their respective triads have been obliterated. R_3 is always detached and is shortened so that it is about as long as IR_2 Along the margin of the fore wing, between each of the principal veins, there are short intercalary veins. The number of these veins in each wing space is either one or two, depending upon the genus under consideration.

After noting the distinctive morphology of each of the genera of this group, we will discuss their phylogenetic relations in the sections concerned with *Cloëon* and *Pseudocloëon.*

Callibaëtis. The hind wing of this genus (Fig. 24) is fair sized and has a number of cross veins present. The fore wing (Fig. 23) also has a goodly number of cross veins. The intercalaries vary in number with the various parts of the wing. In this genus, as in all of the other genera of the family, the genitalia during the nymphal state are almost, if not wholly, lacking as visible external organs. In mature nymphs the genital organs can sometimes be seen through the thin chitin of the ninth sternite. In the case of *Callibaëtis,* however, mature nymphs have tiny cone shaped forceps (Fig. 56).

In the adult state, the genitalia (Fig. 48), as in all the rest of the relatives of this genus, exhibit a peculiar condition in having the styliger plate divided into separate parts. From the posterior ends of these structures arise the 2-jointed forceps, consisting of a long, slender, basal segment and a short, small, terminal segment. The penes are internal (uncertainly extrusible), all evidence of external organs being completely absent.

The mandibles (Fig. 96) are heavy and sturdy with short incisors and large molar areas, the grinding ridges of which are narrow and numerous. The laciniae mobiles are dissimilar (Figs. 179, 180).

The maxillae (Fig. 123) are like the mandibles, *i.e.,* heavy, thick, and sturdy, with strong lacinial dentes and lacinial spurs. The palps are 2-jointed with the segments about the same length.

The labium (Fig. 157) has 3-jointed palps with the first joint longer than the distal two combined. The paraglossae and glossae are finger-like structures arising from the nearly straight anterior edge of the inner lobe. They are about the same size.

The gills in *Callibaëtis* are peculiar structures, differing among different species. In one species (undetermined) the first two (Fig. 218) are triple; the third, fourth, fifth, and sixth (Fig. 217) are double, and the last one (Fig. 218) is single. This type of gill appears to have originated from a lateral extension of a single gill. This extension is supplied with a single branch of the main trachea. In the course of the evolution, this flap became folded at its junction with the main part of the gill giving rise to a double gill. Still later this secondary part in turn gave rise to an extension and thus the triple gill originated. In another species of *Callibaëtis* the triple portion of the first and second gills is very small, while Eaton states that the gills of a species which he had are all double, and Needham describes the nymph of *C. skokiana* as having all of the gills double, the inferior portions becoming progressively smaller on the posterior gills. These double gills would appear to be more primitive than the triple gills.

Baëtis. The cross venation in the fore wings of *Baëtis* (Fig. 17) is greatly reduced. The hind wings (Figs. 19, 20, 27) have been extremely reduced and the costal projection now consists of a small, obtuse, sharply pointed structure, or it is in some instances absent. The hind wing varies greatly in different species of the genus. Thus *B. parvus* Dodds has a large hind wing for a *Baëtis* (Fig. 19). The costal projection is present and, in addition to the usual veins in a baëtid hind wing, MA is to be found as a simple vein attached to the radius. In *Baëtis intercalaris* McDunnough (Fig. 20), the costal projection is present, but MA is lacking. In other species (Fig. 27), the costal projection and the median is lacking.

The genitalia are invisible during the nymphal state (Fig. 73). The adult genitalia (Fig. 65) like that of *Callibaëtis* consist of a divided styliger plate, a 2-jointed forceps, and internal penes. The forceps segments, especially the long basal joints, vary greatly in shape. Usually they are expanded proximally and show incipient segmentation where they contract. In *Baëtis spinosus* McDonnough this basal enlargement is long, and at the point of contraction a distinct shoulder evidences itself on the inner side of the segment. The terminal joint is slender and moderately long.

The mandibles (Fig. 107) are heavy and strong with the enormous canines directed slightly outward and fused to form a single structure. The laciniae mobiles terminate with heavy, rounded teeth.

The maxillae (Fig. 127) like the mandibles are strong and thick, with heavy lacinial dentes and lacinial spurs. The palps are 2-jointed.

The labial palps (Fig. 162) are 3-jointed, the terminal joint being short and terminating roundly. The second joint may be broadly distended distally (*B. pygmaeus,* Fig. 162), or may be of an even size throughout. The paraglossae and glossae arise from the straight anterior edge of the internal lobe. The former are finger-like structures, while the latter are slender, sharply pointed, and somewhat shorter than the paraglossae.

The gills (Fig. 220) which are to be found on abdominal segments one to seven are single, sub-oval, foliaceous structures, each with a pinnately branched trachea. In the case of *B. pygmaeus,* the terminal gill is broadly lanceolate.

Pseudocloëon. The genus *Pseudocloëon* (Figs. 18, 70) is like *Baëtis* in every item of nymphal and adult structure considered here, except that the adult lacks hind wings and the nymph has only two caudal setae. McDunnough has established a genus *Hetercloëon* (of which the nymphs are also unknown), for those species in which the hind wings are present but are reduced to a mere thread. What the nymphs of these two genera are like can only be hypothesized. Considering wing characters alone, a graded series can be found which extends from the condition found in *Baëtis parvus* to that found in *Pseudocloëon.* Bengtsson (1912) established the genus *Acentrella* for those species in which the hind wing lacks the costal projection and possesses only two longitudinal veins, *i.e.,* the Sc and R. In the present paper neither *Acentrella* nor *Hetercloëon* are accepted as good genera, but are treated as elements of true *Baëtis.* It is possible that even *Pseudocloëon* should be considered part of the genus *Baëtis,* comparable with the short winged forms known among *Drosophila,* leaf hoppers, beetles, parasitic hymenoptera, gall wasps, etc. (See Kinsey, 1930.) Each of the types of reduced wings in these mayfly groups may have arisen by direct and independent mutation from a form such as *B. parvus.* It is not necessary that there has been a gradual decrease in the size of the hind wings. The *Pseudocloëon* species *may* be more closely related to a species of *Baëtis* than are two species which are now unquestionably regarded as members of that genus.

A thorough and careful working of the whole group with large series from wide localities, plus the correct association of the nymphs with the adults, may throw some light upon the question of relationships and the relative positions of the various species in the evolutionary scheme. Until that time it is necessary to admit that our classification may be and probably is an artificial one, and that it can not be said with certainty that it represents a picture of the phylogenetic history of the group.

Centroptilium. The fore wing of *Centroptilium* (Fig. 25) is similar to that of *Baëtis* except that only one intercalary is to be found in each marginal wing space. The hind wing (Fig. 28) is long, slender, and very narrow with an acuminate costal projection.

The genitalia (Fig. 69), while basically like those of *Baëtis* and *Callibaëtis* during both the nymphal and adult stages, show distinctive differences in the adult in having the terminal segment small and droplet shaped, while the first or proximal segment is expanded at its termination. The styliger plate is divided. The penes are external, being represented by small, hump-like structures. They show no indication of being double. In only a few species of this genus have the nymphs and adults been associated. Eaton has figured *C. lutelolum* which he connected to the proper adult by field observation and possibly by rearing. McDunnough has connected the nymph of his *C. album* with its adult, and Ide has identified the nymphs of *C. convexum* Ide and *C. bellum* McDunnough.

There is goodly variation between these nymphs in regard to mouth parts and gills. Only by extensive rearing of many species will the problem be completely cleared up.

The mandibles (Fig. 99) and also those described for *C. lutelolum* are more like generalized mandibles than are those to be found in *Baëtis.* The canines are not fused, and the laciniae mobiles are distinct. In one species of *Centroptilium,* however, the mandibles are similar to those of *Baëtis.*

The maxillae (Fig. 122) are also more generalized in shape and ornamentation than those of *Baëtis.* In *C. album* and *C. lutelolum* the palps are 3-jointed, but in *C. convexum, C. bellum,* and *C. sp.* they are only 2-jointed with the terminal joint long and slender.

The labium (Fig. 150) has the glossae and paraglossae about equal in size, with the glossae terminating sharply and the paraglossae slightly curved. They arise from the slightly bulging internal lobe. The palps are always 3-jointed with the terminal joint expanded, short, and truncate. This truncate, last segment of the labial palp is one of the primary means of identifying *Centroptilium* nymphs. In *C. bellum,* however, the terminal margin of this segment is slightly oblique.

The gills, like the mouth parts, are variable. Eaton has figured the gills of *C. lutelolum* as being similar to those of *Baëtis* except that they terminate acutely. This, along with the characteristic labial palp, has been employed as a primary means of identification. On the other hand, in *C. album* and *C. convexum* they are broadly rounded, and in other species (Fig. 213) they become broadly expanded distally so that the gills are somewhat triangular in shape. In *C. bellum* and an undetermined species (Fig. 221) all seven gills possess a slender lateral flap that has been folded back so as to create a double gill. It is impossible to say at present whether this heterogeneous group of nymphs really represents a single, phylogenetic unit. It is perfectly plausible that the nymphs have undergone mutations while the adults have remained the same, and this seems a reasonable explanation for the variations cited above.

The gills in this group of genera, as was apparent in *Callibaëtis* and *Baëtis,* and as will hold true for *Cloëon,* are highly variable structures.

Cloëon. Concerning the wings and genitalia of the adults, this genus (Figs. 26, 64) is an exact duplicate of *Centroptilium* except that it completely lacks a hind wing.

The mandibles (Fig. 103) are much like those of *Baëtis.* The maxillae (Fig. 126) have 2-jointed palps with segments like those in *Centroptilium.*

The labium (Fig. 154) shows distinct relationship to *Centroptilium* except that the terminal palp segment is obliquely truncate.

The gills are roughly oval (*Cloëon simile* Fig. 212) or sub-oval (Fig. 214), and have a lateral flap on gills one to six which has been folded parallel to the main body of the gill so as to form a compound gill. McDunnough states that this lateral flap is present on the seventh gill of *C. igens,* but it is lacking on *C. mendax* according to Ide and also according to my own observations.

Thus, within this compact group of genera, it is possible to distinguish three distinct lines of evolution. *Callibaëtis* represents one line, which is the most primitive of the three; the other two branches are highly specialized and about equal in position. *Baëtis* and *Pseudocloëon* make up one line and *Centroptilium* and *Cloëon* the other. If some of the related, monotypic genera are to be considered as valid, then *Hetercloëon* and *Acentrella* must be added to the *Baëtris* branch and *Procloëon* and *Centroptiloides* to the *Centroptilium* branch.

Bengtsson (1914) has discussed the phylogeny of this group, but while he recognized the distinct line of evolution represented by *Callibaëtis,* he derived *Callibaëtis* from *Baëtis,* and failed to recognize two distinct lines of evolution and has placed all of the remaining genera in a linear arrangement.

Super Family EPHEMEROIDEA

Family *Leptophlebidae*

Blasturus, Leptophlebia, Choroterpes, and *Thraulus**

These four genera show decided relationships, and may be discussed together. They stand comparatively low on one of the main branches of the evolutionary tree of the mayflies.

Blasturus, which is probably the most primitive genus of the group, shows distinctive characters in the venation (Fig. 31). The R_3 has become completely detached at the base from R_2. The connection of MP_2 to MP_1 is weak. All traces of the CuA triad have been lost, and between CuA and CuP a pair of interpolated veins is to be found. CuP pursues a fairly straight course in the Heptageniidæ, Baëtidæ, and *Siphlonurus,* but is strongly arched in *Blasturus.* At its base it lies midway between CuA and A_1 but within the wing root it swings sharply forward and joins CuA_1. The anal area is small and only A_1, and A_2 with the interpolated vein IA_1 are present; A_1, however, is attached basally. In the hind wing (Fig. 32) the Sc displays the primitive condition of being moderately arched; R_1 and MA, however, are fused for some distance; MA is unbranched, and a pair of interpolated veins lie in the CuA area. The hind wing is moderately large in comparison with the front wing.

Thraulus has greatly reduced hind wings (Fig. 30) and consequent with this reduction there has been a shifting of some veins and a complete suppression of others. The differences between the fore wing of *Thraulus* (Fig. 29) and *Blasturus* are restricted to the cubital and anal regions, and can be accounted for by the reduction of the hind wing and the consequent moving of the anal angle nearer the wing base. This has in turn been

* Upon further study, I have become convinced that the adult specimens utilized for this paper as representatives of *Choroterpes* belong to the genus *Thraulus* rather than to *Chroroterpes.* In reading the first section of this paper (N. Y. ENT. SOC., 41: 55–86), the reader should bear this correction in mind In the following discussion, the reader will note that I lack nymphal material for *Thraulus* and adult material for *Choroterpes.* The two genera seem to be so closely related, however, that I feel certain my phylogenetic placement of them is correct.

accompanied by an enlargement of the cubital area and a reduction of the anal area.

The wing of *Leptophlebia* (Fig. 21) displays a venation and shape intermediate between that of *Thraulus* and *Blasturus,* but is closer to *Blasturus* than to *Thraulus.*

The genitalia of *Blasturus, Leptophlebia,* and *Thraulus* are much alike. During the mature nymphal stages, the styliger plate (Figs. 74, 78, 80) is a cone shaped structure which bears unjointed forceps on its sloping sides. The nymphal penes, which are hidden by the styliger plate, consist of two small finger-like structures which lie side by side. In the adult state, the styliger plate of *Thraulus* (Fig. 63) is narrow (antero-posteriorly, not laterally), with only a slight prominence along the posterior edge. This prominence is slightly indented at the middle. In *Blasturus* the styliger plate has been greatly extended postero-medially (Fig. 72) and is deeply incised along the middle, though it is not completely divided into two elements. The species of the genus *Leptophlebia* (Fig. 68) exhibit a variable condition intermediate between that found in *Blasturus* and *Thraulus* not only in reference to the styliger plate but also in reference to the penes. Some species are like *Blasturus,* while others approach the condition found in *Thraulus.* The penes in *Blasturus* (Fig. 72) consist of two straight, posteriorly directed, rod-like processes which lie side by side. From the postero-dorsal surfaces of each of these bodies there arises a strongly arched, inwardly concave, slender, tail-like process which is directed anteriorly. The penes of *Thraulus* (Fig. 63) are similar except that the tail-like processes are lacking. *Leptophlebia* (Fig. 68), as mentioned above, exhibits an intermediate condition.

The forceps of *Blasturus, Leptophlebia,* and *Thraulus* in the adult condition are 3-jointed with long, tapering basal joints and two short terminal segments of which the penultimate is the heavier and longer (Figs. 63, 68, 72). Thus these genera lack the basal articulation so characteristic of the Heptageniidae and *Siphlonurus.* Another peculiarity of the forceps is that they arise from the dorsal surface of the styliger plate and that the latter extends under them for a short distance posteriorly.

Usually in most genera the forceps arise from the posterior edge of the styliger plate.

The maxillary (Figs. 129, 131, 132) and labial palps (Figs. 151, 155, 160) of these genera are all 3-jointed, with the first joint always the longest and sturdiest. They are all slender, cylindrical and unexpanded. The lacinia-galea is expanded (Figs. 129, 131, 132), and on its terminal edge the lacinial portion bears a dense patch of setae. The lacinial dentes are small and the spines on the inner surfaces are restricted to the vicinity of the dentes.

As regards dentation and form, the mandibles in *Leptophlebia* and *Blasturus* are similar (Figs. 112, 115), while those of *Choroterpes* (Fig. 111) show some but not as close relationship.

The laciniae mobiles (Figs. 175, 176, 177, 178, 181, 182(also show distinct relationships between the three genera.

The paraglossae (Figs. 151, 155, 160) are expanded, especially in *Choroterpes,* so that they roughly resemble a quadrant of a circle. In *Choroterpes* the extreme development of the paraglossae has resulted in small, reduced glossae (which are short, finger-like bodies located between the paraglossae), while in *Blasturus* and *Leptophlebia* the paraglossae are not so decidedly expanded and the glossae are larger and more expanded, especially posteriorly, and slightly ventral in position in relation to the paraglossae.

The gills of *Leptophlebia* (Fig. 228) are double organs which consist of two blade-like lamellae which join basally forming a Y-like structure. Into the gills runs a single trachea which gives off a limb to each lamella. All seven pairs of gills are similar in construction. In *Blasturus* the first gill (Fig. 227) is identical with the gills of *Leptophlebia.* The remaining gills, however, have had the basal two-thirds of both lamellae broadly dilated (Figs. 225, 226), while the distal third has the same appearance as the distal part of the *Leptophlebia* gills, *i.e.,* a slender, blade-like lamella. The basal parts of the last six gills of *Choroterpes* (Figs. 222, 223) are also broadly expanded, while the distal third is expanded but not as greatly as the proximal parts Between the distal and proximal parts the gill contracts strongly, and the distal part has become twisted so that this part of the gill lamellae stands at right angles to the basal section. The first gill of *Choroterpes* (Fig. 224) consists of a single blade-like lamella.

From the above discussion it is evident that *Leptophlebia* and *Blasturus* present a closer affinity to each other than they do to *Thraulus* and *Choroterpes* although all four genera form a closely knit group. Indications that they all represent primitive branches of a major division of the Ephemerida are: (1) the fairly primitive condition of the wings, especially those of *Blasturus;* (2) the simple form of double gill consisting of two foliaceous lamellae without such special modifications as are found in the Heptageniidae and *Baëtidae* branches; and (3) the 3-jointed forceps, lacking any indications of the basal articulation commonly found elsewhee in the order.

Ephemeridæ

Potamanthus. This genus clearly stands intermediate between the genera *Blasturus, Choroterpes,* and *Leptophlebia* and the rest of the Ephemeridæ. Many of its characteristics connect it definitely with the Ephemeridæ while others undoubtedly indicate a derivation from the same stock from which *Blasturus* and its relatives arose.

The wing venation (Fig. 34), definitely places it as a close relative to *Hexagenia* (Fig. 41), *Ephemera* (Fig. 39), *Polymitarcys* (Fig. 43), *Pentagenia* (Fig. 37), and *Campsurus* (Fig. 38). In the fore wing there seems to be a tendency toward the elimination of R_3 and IR_2 not only in *Potamanthus* but also in the other Ephemeridæ. The R_3 (Fig. 34) has lost its true basal attachment to R_2 and is now connected by a cross vein. The point of attachment, via the cross vein, is now much further from the base of the wing than it is in the primitive condition. Accompanying this there has been a reduction in the length of IR_2 and the branches of the R_3 triad. The posterior median and cubital veins have undergone distinctive specialization. MP_2 has lost its true basal attachment and this rôle has been assumed by a cross vein, thus creating an obtuse angle between MP_2 and MP_1 (Fig. 34). This peculiar behavior of the posterior median is the chief character which is used to define the family Ephemeridæ. CuA and CuP have migrated anteriorly and immediately after their union they join MA_1. Distally CuA is arched as in *Blasturus* and this, plus the decided anterior migration of the proximal part, has caused CuA_1 to pursue a sigmoid course. CuP is also sigmoid but to a lesser degree. Between the cubital veins a number of posteriorly directed pectinates are to be found. A_1 is distinctly present and has been carried forward, but IA_1 and A_2 have not been prolonged anteriorly. The anal region is smaller than in *Blasturus*.

In the hind wing (Fig. 35), as in *Blasturus* and in the other Ephemeridæ, R_1 and M are fused for a short distance and the MA is unbranched. The callus, however, apparently has migrated outwardly from its usual position which it occupies in the more primitive genera and forced the cubital veins apart.

While the wings of *Potamanthus* display a close relationship to the remainder of the Ephemeridæ, the genitalia (Fig. 77) show an equally distinct relationship to the Leptophlebiidæ. The condition of the genitalia (Fig. 79) in mature nymphs clearly indicates an intermediate condition between that found in the remainder of the Ephemeridæ and the Leptophlebiidæ. The forceps are 2-jointed, the styliger plate is roughly cone shaped, and the penes show a certain amount of fusion on their inner sides.

In the adult state (Fig. 77), the forceps are only 3-jointed, there being no basal articulation present which, as shall be shown later, is possessed by all the rest of the Ephemeridæ. The proportions and shapes of the various segments of the forceps are the same as those in *Blasturus* (Figs. 63, 68, 72) and its relatives. The penes are somewhat like those of *Blasturus* except that they lack the recurvant, finger-like process, and are expanded terminally, but assuredly they are more like the type found in *Blasturus* than any that are found in the remaining Ephemeridæ.

Concerning the mouth parts, the mandibles (Figs. 104, 108) are tusked as in the rest of the Ephemeridæ, but the dentation of *Potamanthus* has not undergone the shifting of position to which the incisors and molars of the other Ephemeridæ have been subjected.

The laciniae-mobiles (Figs. 186, 187) are distinctly similar to those in *Blasturus* (Figs. 175, 176) ; it should be noted that there is variability in the laciniae of the various genera. The left lacinia mobilis in *Potamanthus* represents a type intermediate between that found in *Blasturus* (Fig. 176) and *Hexagenia* (Fig. 190).

The maxillary palps (Fig. 133) are 3-jointed and the segments compare in shape to those of *Blasturus* (Fig. 129) except that the terminal segment has become elongated and the second segment is reduced. The shape and ornamentation of the lacinia-galea approximate those of *Blasturus* except that the whole organ is more slender than it is in *Blasturus.*

The labial palps (Fig. 159) of *Potamanthus* are similar to the maxillary palps. The glossae and paraglossae (Fig. 159) are more expanded laterally than those of *Blasturus.*

The gills of *Potamanthus* (Fig. 229) display the basic plan that is exhibited by the Leptophlebiidæ but, instead of the gill lamellae expanding as in *Blasturus* (Figs. 225, 226) and *Choroterpes* (Figs. 222, 223), *they have developed a number of laterally directed filaments.*

From the above discussion it is evident that *Potamanthus* (by virtue of the wings, the tusks of the mandible, and the gills) is related to the burrowing Ephemeridæ on one hand; while the genitalia, mouth parts, and the gills connect the genus with *Blasturus* and its relatives. The habitats of the various genera also lead to the same interpretation of relationships. *Blasturus, Leptophlebia,* and *Choroterpes* live on the bottom and crawl around in the debris, while *Potamanthus* is a semi-burrower and lives under stones and shells and other objects of like character on the bottoms of the streams. The remainder of the Ephemeridæ are true burrowers.

Hexagenia, Ephemera, Polymitarcys, Pentagenia, and *Campsurus.* The Ephemeridae or burrowers in North America consist of five genera besides *Potamanthus, i.e., Hexagenia, Ephemera, Polymitarcys, Pentagenia,* and the extraordinary stump-legged genus *Campsurus.* I do not possess nymphs of *Campsurus* so its relative position has been based upon the two adult characters, wings and genitalia. The stump-legged condition, however, is sufficient to show that, while its nearest relatives are undoubtedly the other burrowers, it stands distinct.

The wings of these genera (Figs. 37, 38, 39, 41, 43) are similar to those described above for *Potamanthus* except in a few features. In the fore wing the CuA always joins the MP before it joins CuP. *Pentagenia* has the R_3 and its triad more reduced (Fig. 37). The genus *Polymitarcys* is distinct by virtue of the copious cross venation of its wing (Fig. 43) and the enlarged CuA area which lacks the posteriorly directed pectinates that are to be found in the other genera, but which does have two pairs of interpolated veins in the CuA area. From the fourth of these veins arises a series of pectinates, and the MP_2 always fuses with CuA before it joins MP_1. In the secondaries of this genus, the callus has retained the primitive position, while the radius and anterior median are unfused. In *Campsurus* (Fig. 43) the R_3 is unbranched in the male, due probably to the complete disappearance of R_{3a}, while in the female both R_3 and IR_2 are absent. The forking of the MA_1 has receded to the wing base, and the basal part of MP_2 has been lost so that the vein is now attached by a cross vein to IMP a goodly distance out from the wing base. The costal area has been greatly reduced and only a single pectinate vein runs posteriorly from CuA, while a sturdy cross vein is found between A_1 and CuP. A_1 is the only anal vein present. In the hind wing of the male (Fig. 44) R_3 is unbranched just as it is in the hind wing of the female.

The genitalia of each of the above mentioned genera are distinctive. Within each genus the various species exhibit structures much alike, but between genera (even though they are closely related) there is an enormous amount of difference. During the mature nymphal state *Ephemera* (Fig. 81), *Hexagenia* (Fig. 85), and *Polymitarcys* (Fig. 86) agree, however, in having (1) a 3-jointed forceps, which consists of a short basal joint, a long second joint, and a short terminal joint; (2) small, ribbon-like styliger plates; and (3) externally visible forceps due to the reduction of styliger plates. I do not have enough material of *Pentagenia* to draw conclusions. In the adult state all of these genera agree in one point, *i.e.*, the forceps possess a basal articulation, and thus are 4-jointed in *Ephemera* (Fig. 71), *Hexagenia* (Fig. 76), *Polymitarcys* (Fig. 83), and *Pentagenia* (Fig. 82). These forceps consist of a short, sturdy basal joint and a long, slender second joint. Finally, segments three and four are relatively short and small. This definitely distinguishes these genera from *Potamanthus* which lacks all indications of a basal articulation. In *Campsurus* (Fig. 84), however, while the basal articulation is present, the terminal segments have been lost so that the forceps now consist of a short basal segment and a slender second joint which has become expanded on the terminal end. The styliger plate (Figs. 71, 76, 82, 83, 84) and penes proper present great differences between the various genera and do not serve as indicators of relationships.

The mandibles in these genera (Figs. 105, 106, 109, 110) are all tusked. This acquisition of tusks has been accompanied by the shifting and twisting of the molars and incisors. Thus the molars and incisors retain the same position as in primitive genera, even though the long axis of the mandibles has shifted from a perpendicular to a horizontal position.

The laciniæ mobiles bespeak an affinity between *Ephemera* (Figs. 193, 194) and *Hexagenia* (Figs. 189, 190) on one hand and *Polymitarcys* (Fig. 191) and *Pentagenia* (Fig. 195) on the other, with the former two closer than the latter.

As in *Potamanthus* the maxillary palps are 3-jointed, except in *Polymitarcys* (Fig. 134) where they are 2-jointed. The maxillæ, by virtue of their long slender palps and the slender, curved, sharply pointed lacinia-galea, indicate close relationships between *Hexagenia* (Fig. 138) and *Ephemera* (Fig. 139), while on the basis of this criterion *Polymitarcys* (Fig. 134) and *Pentagenia* (Fig. 140) are rather distinct.

The glossæ, the paraglossæ, and the internal lobes of the labium in *Pentagenia* (Fig. 156), *Ephemera* (Fig. 153), and *Polymitarcys* (Fig. 152) are similar to those found in *Potamanthus* (Fig. 159) as described above. In *Hexagenia* (Fig. 161), however, the postero-lateral area of the paraglossae has been produced until the point of attachment of the internal lobe lies on a midpoint on the inner surface of the paraglossae. Anteriorly the tips of the paraglossae almost touch since the glossae have been greatly reduced. The palps of the labium are 3-

jointed in *Polymitarcys* (Fig. 152) and *Ephemera* (Fig. 153), while in *Hexagenia* (Fig. 161) and *Pentagenia* (Fig. 156) they are 2-jointed.

The gills of these genera, like those of *Potamanthus,* are double, consisting of two blade-like lamellæ with filaments around the periphery. The first gill, however, is always very small, simply consisting of two blade-like lamellæ in *Ephemera, Hexagenia* (Fig. 230), and *Polymitarcys,* becoming a single leaf-like structure in *Pentagenia* (Fig. 239). The shape of the gills and the arrangement of the lamellæ indicate close affinities between *Hexagenia* (Figs. 231, 232) and *Ephemera* (Fig. 238) on one hand and *Pentagenia* (Figs. 233, 234) and *Polymitarcys* (Fig. 243) on the other.

Thus, to sum up, *Hexagenia* and *Ephemera* are closely related, constituting one of the evolutionary branches which has divided recently into these two genera. *Campsurus* represents another stock. *Pentagenia* and *Polymitarcys* are close relatives and represent still another stock, although they are more distinct from each other than *Ephemera* and *Hexagenia* are from one another.

Potamanthus stands as an intermediate between the other Ephemeridæ and the Leptophlebiidæ. The latter family represents an off-shoot from a primitive stock, the genera of which have been considerably modified since its origin. This primitive stock apparently had the genital forceps 3-jointed, while the penes were rod-like structures, lacking both spurs and parameres. The wings were somewhat primitive but showed certain specializations, such as the reduction of the anal area, the bending posteriorly of the Cu_2 and the detachment of R_3. The nymphs were bottom dwellers and crawled around on the bottoms of streams. The mouth parts in all probability were like those found in the Leptophlebiidæ genera today. The gills probably resembled those of the present day *Leptophlebia.* Thus, they did not possess any special protection for their gills, nor were the gills capable of a great amount of movement so as to be able to keep up a circulation of water around them. The nymphs, which were probably poor swimmers, should have lived in fairly clear, well aerated water, and were probably excluded from swift-flowing streams which carried a large amount of heavy material that would have injured the delicate gills. They could not have lived in the muck bottoms inhabited by the present day *Tricorythus.* After the origin of the Leptophlebiidae, the main stock underwent three morphological changes that were of great importance and one ecological change. The mandibles developed tusks; the wings developed the peculiar characteristics of the M, Cu, and anal veins of the Ephemeridæ, while the gills changed from the simply compounded type to something like that found in *Potamanthus* at the present time. At the same time the nymphs began a semi-burrowing existence. An individual of this primitive stock possibly looked like the present day *Potamanthus,* except that the primitive nymph was cylindrical in shape.

With the development of the tusks and the change in position of the incisors and molars, the nymphs became true burrowers. In the adult a basal articulation of the forceps of the genitalia was developed, so that these organs became 4-jointed.

Family Ephemerellidæ

Ephemerella

Ephemerella, along with *Tricorythus,* occupies a distinct and separate place in the phylogenetic story. The wings (Figs. 55, 47) show a relationship to *Blasturus,* but the position of the Cu veins basally and the strong arching of the CuA and A_1 indicates a different type of specialization of the fore wing. The anal vein, especially, differs from that of *Blasturus.* The hind wing of *Ephemerella* (Fig. 55) is somewhat specialized in having the Sc strongly arched, the cross venation reduced, and the sinus on the anterior margin indicating an incipient reduction of the wing.

The adult forceps (Fig. 88) are distinct, for while they are 3-jointed, as they are in *Blasturus,* in *Ephemerella* the three segments consist of a short, heavy basal part, a long, slightly concave second segment, and a heavy and oval terminal member. It is possible that this type of forceps arose from the type found in *Blasturus* (Fig. 72) and its relatives, by the long basal joint of the latter developing an articulation near the base, and by the loss of the terminal joint. The condition of the genitalia of *Ephemerella* during the nymphal state also substantiates this explanation. The genitalia of mature *Ephemerella* nymphs (Figs. 92, 93) show such close resemblance to those of *Blasturus* (Fig. 74) as to warrant this belief. In both instances the styliger plate is cone shaped with small, finger-like, unsegmented forceps arising from its sloping sides. We have seen that in *Campsurus* a parallel development has taken place, except that in *Campsurus* both terminal joints have been lost.

The penes (Fig. 88) is a simple, tubular affair which is incised at the tip. This penes obviously originated by the fusion of the two penes of the primitive stock. This is substantiated by the fact that the nymphal penes consist of two separate structures. The styliger plate is deep and the posterior edge may be arched or almost straight.

The mandibles (Fig. 113) are distinctly like those of *Blasturus.* The outer edges are more nearly straight and the body of each mandible is more slender, but in fundamental shape and dentation they are much like those of *Blasturus.* The laciniae mobiles (Figs. 188, 192) are much alike in the two genera.

The maxillae are peculiar. The maxillary palps are generally 3-jointed (Fig. 135), but the palps are small and weak and in the bicolor group (Fig. 136) completely lacking. The lacinia-galea (Figs. 135, 136) is massive and thick. The lacinial dentes and lacinial spurs are heavy and strong; the setae on the lacinial and galeal surfaces and the lacinial spurs are restricted to the terminal area of the lacinia-galea.

The labium (Figs. 164, 165) is likewise distinctive. The submentum is greatly expanded, and the internal lobe has been enlarged at the expense of the glossæ and paraglossæ which are small. The labial palps are 3-jointed, with the first segment heavy and large, the second smaller, and the third very small.

The gills of *Ephemerella,* along with those of *Tricorythus,* are the most complex and distinctive within the family. Each gill consists fundamentally of a double gill of which the anterior member (Fig. 242), a heavy, foliaceous structure, serves principally as a protecting shield, although it also receives a tracheal branch and doubtless carries on some respiration. The posterior gill member (Figs. 237, 240) consists of a foliaceous structure that has acquired a double row of finger-like processes, one row on each side of the gill lamellæ. These large, postero-laterally directed processes have greatly increased the area of the lamella. This member may be secondarily divided again at right angles to the plane of division between the principal gill lamellæ (Fig. 237). This secondary division is not as well developed in the posterior as in the anterior gills. The most posterior gill (Fig. 240) lacks all indication of cleavage. If there is a gill on the first segment, it is simply a slender, elongate member (Fig. 244). The gill on the second abdominal segment is invariably absent and there are some species in which even the third segment may lack a gill. The absence of gills on segments two and three, as in the *bicolor-lutulenta* complex, in *Ephemerella,* and in *E. margarita,* represents specialization greater than that found in species that lack gills only on the second abdominal segment (as in *E. inermis, E. aronii,* and *E. cornuata*). Nymphs of the latter species have gills which are closely imbricated on the dorsum of the abdomen. In the *bicolor-lutulenta* complex, they are more or less stratified, and the protective portion of the first gill almost completely covers all the remaining gills.

Various attempts have been made to split up the genus *Ephemerelle.* Bengtsson (1909) erected the genus *Chitonophora;* Needham (1905) created *Drunella,* and in 1928 segregated the two subgenera *Eatonella* and *Timpanoga.*

All these divisions are open to serious criticisms, due primarily to the fact that they are based upon nymphal material. Not until the adults of the various species have been correctly connected to their nymphs is it going to be possible to determine the relationships and the phylogenetic story within the group. Consequently, in this paper the genus *Ephemerella* has been considered in the sense of including all of the above mentioned divisions.

Tricorythus

The genus *Tricorythus,* while clearly distinct from *Ephemerella,* is more closely related to it than to any other genus of the family.

This genus is greatly specialized. It possesses only one pair of wings, the hind wings having been completely lost. Along with this loss, the anal area (Fig. 46) has been so enlarged that the anal angle has completely disappeared. There seems to be a tendency for each vein to attach to the next posterior vein. With the loss of the anal angle and the expansion of the anal area, the placement of the major veins has been shifted. CuP now joins A_1 at the base, and MP_2, which had a very weak attachment in *Ephemerella,* has become completely detached. The cross venation has been restricted to the inner part of the wing disk.

As in *Ephemerella,* the genitalia in *Tricorythus* have 3-jointed forceps in the adult state (Fig. 87), consisting of a short basal joint; a long second segment which has a spherical protuberance on its inner proximal surface; and a short, rotund terminal segment. The styliger plate is moderately long, but is deeply excavated medianly while the penes consist of a tubular organ (Fig. 87) that apparently has risen from the fusion of the two penes just as in *Ephemerella.* In mature nymphs the genitalia (Fig. 94) also show a distinct relationship to *Ephemerella.*

The mandibles (Fig. 114) are much like those of *Ephemerella* in regard to the shape, the dentation, and the lacinia mobilis. The maxillæ (Fig. 137) and the labium (Fig. 158) likewise exhibit unmistakable affinities to *Ephemerella.* The glossæ and paraglossæ have been reduced to an even greater extent than in *Ephemerella.*

The gills which are located on abdominal segments two to six are complex, just as in *Ephemerella,* with an anterior lamella (Figs. 245, 249) of each gill modified so as to form a protective shield, and the posterior lamella adapted primarily for respiration. The posterior lamella (Fig. 241) consists of two foliaceous parts which overlap each other. The gills assume a stratified position, *i.e.,* the first gill (Fig. 249) entirely covers the remaining gills. The ancestors of *Tricorythus* probably had imbricated gills, judging from the structure of the anterior member of each gill. Now, however, the gills are stratified, the foremost gill serving as a shield for all the other gills, and the inferior part

(Fig. 248) of the first gill is so modified that it, in connection with the shield portion, forms a sort of gill box.

Formerly this genus has been considered as a relative of *Cænis,* based upon the fact that both genera lack hind wings, and nymphs of the two genera show a striking, although superficial, resemblance. As will be shown in the discussion on *Cænis,* these similarities have arisen independently of each other.

Some will doubtless advance the argument that the great similarities between the mouth parts of *Ephemerella* and *Tricorythus* are parallel adaptations of the nymphs to somewhat similar habitats. This is possible, but there are similarities in other structures in these insects which seem certain evidence of actual relationships. The genitalia of the two groups are similar and very distinct from the genitalia of other members of the family. Nevertheless, the differences between the gills and the wings of these genera are enough to suggest that the two have been distinct for some time.

The *Ephemerella* and *Tricorythus* branch probably arose from the stock which later broke up into the genera *Blasturus, Leptophlebia,* and *Choroterpes,* and the family Ephemeridæ. The wings of *Ephemerella* show a closer resemblance to those of *Blasturus* than to any other extant genus. The genitalia of the adults of these two genera, it is true, are quite different, but the similarities of the nymphal genitalia between *Blasturus, Leptophlebia,* and *Choroterpes* on one hand and *Ephemerella* and *Tricorythus* on the other hand can not be disregarded. The mandibles of *Ephemerella* also show a distinct likeness to those of *Blasturus.* Superficially the gills of the *Ephemerella-Tricorythus* stock are very different from the type found in the *Blasturus, Leptophlebia,* and *Choroterpes.* Fundamentally, however, the differences are not great. The *Ephemerella* gill is a double structure of which the inferior lamella of the anterior gills has become secondarily split. The seventh abdominal gills, however, lack this secondary splitting, and each gill consists of a double structure whose lamellæ are greatly expanded and thus basically does not differ from the gill of *Blasturus.*

Ephemerella-Tricorythus represent a branch of generalized stock described at the end of the section dealing with the Ephemeridæ, which probably originated earlier than the stock represented by *Blasturus* and its relatives. Instead of becoming burrowers as the Ephemeridæ have done, or still living in a habitat very similar to that of their ancestors as *Blasturus* has done, the *Ephemerella-Tricorythus* stock became dwellers in and amongst the vegetation and gravels of swiftly flowing waters. Accompanying this the gills became reduced and the superior gill lamellæ developed protective features. The lacinia-galea became heavy and sturdy; the maxillary palps were reduced in size; and the paraglossæ and glossæ decreased in size, while the internal lobe became large. Since the origin of this stock, the forceps of the adult genitalia have developed the basal segmentation, and the penes have become more or less fused together.

Super Family Cænoidea

Family Cænidæ

Cœnis

As mentioned before, *Cœnis* has been considered a close relative of *Tricorythus,* because of the superficial external similarities of the nymphs and adults of the two genera; but *Tricorythus* appears to have been derived from the same stock as the Leptophlebidæ-Ephemeridæ stock; and although we are not certain of the ancestors of *Cœnis,* the distinctive character of the latter genus shows this type of classification to be absurd. The distinctive characters of *Cœnis* indicate that it has been removed from the rest of the order for a very long time. *Cœnis* (Fig. 45) differs from *Tricorythus* in that MA_2 is broken away from M, and MP_2 and IMP are distinct veins that originate in the wing base. The CuP is attached to A at the base, which is the only anal vein present. The cross venation has become reduced to a uniserial condition.

The genitalia (Fig. 89) of *Caenis* are the most peculiar in the order. During the nymphal stage the genitalia are internal. In mature nymphs (Fig. 90) the forceps and penes can be discerned through the thin chitin of the ninth sternite. The penes appear as a rectangular organ located near the anterior end of the sternite. The forceps seem to be unsegmented and arise lateral to the penes. Posteriorly they extend past the main body of the ninth sternite and are enclosed in the lateral margins of a mound shaped, posterior extension of the sternite. In the adult the styliger plate is small and narrow, and it is produced laterally into slender, arm-like structures. From the end of these arms arise slender, unsegmented, rod-like forceps. The penes (Fig. 89) consist of a single roughly rectangular organ.

The mandibles (Fig. 117) are quite generalized, but they are heavier than the mandibles in most of our genera. The maxillary palps (Fig. 141) are 3-jointed, with the segments strong and large. The lacinia-galea is slender, roughly cylindrical with the lacinial spurs restricted to the terminal end.

The labium (Fig. 196) is of the generalized type, with three segments to the palpus, and the glossae and paraglossae are distinct and unexpanded. The internal lobe is small and unmodified. Thus the labium simulates the labium of *Siphlonurus* (Fig. 143).

Gills are to be found on the first six abdominal segments. The first gill (Fig. 251) is rudimentary, consisting of a seta-like organ. The second is a simple, foliaceous, elytroid-like gill (Fig. 250). It covers all the remaining gills and serves as a protective shield. The other gills (Fig. 246) are foliaceous structures, fringed with unilaterally branched filaments.

Briefly, *Caenis* differs from *Tricorythus* in the venation, in the structure of the mouth parts (especially the labium), in the genitalia, and in the gills. The gills, it is to be remembered, are complex in *Tricorythus*, lack all filamentation, and are not single and filamented as in *Caenis*. Apparently the ancestoral stock from which *Caenis* arose differentiated long ago, and it has since then become highly specialized. In doing so it has reached, both in the nymphal and adult stage, a condition superficially—but only superficially—like that in *Tricorythus*.

Super Family Bætiscoidea

Family Bætiscidæ

Bætisca

The wings (Fig. 54) of this genus are peculiar. The R_2 and R_3 veins form a perfect triad. The branching of the posterior median into its two component parts does not take place as usual, but all three veins (MP_1, IMP, and MP_2) are separate and distinct veins which originate in the wing base. CuA is an unbranched vein, and both CuA and CuP terminate on the outer wing margin, just as in the primitive *Triblosoba.* In all other present-day forms which have two pairs of wings and possess an anal angle, the CuP terminates behind the anal angle. The anal area in *Bætisca* is consequently large. Even though A_1 terminates on the outer margin, there are only two anal veins present.

The hind wing is large and greatly expanded. The subcostal arc is moderate and the radius is weak, extending inward from the margin only about half way to the wing base, thus becoming completely detached. The R_3 gives rise to the usual triad, but the anterior limb has become detached. MA_1 is an unbranched vein, while the anal area exhibits three anals which are all unattached basally.

I lack sufficient nymphal material to draw conclusions as to the nymphal condition of the genitalia. In the adult state (Fig. 75), the styliger plate of the genitalia is rectangular, while the forceps are 2-jointed, with a long, arched, proximal joint which is very broad at the base and contracted sharply about two-fifths of the distance from the base. The terminal segment is short and oval. The penes (Fig. 75) consist of a cone shaped organ which is divided terminally.

The mandibles (Fig. 116) represent a somewhat unspecialized form. The two laciniae mobiles (Fig. 167) are similar—a peculiarity displayed by only one other genus of the order; and in both cases this probably represents a primitive condition. The dentation and shape of the mandible exhibit no extraordinary characteristics. The maxillary palps (Fig. 144) are 3-jointed with an indication of incipient segmentation on the terminal segment. The lacinia-galea (Fig. 144) is heavy but unspecialized as to shape, possessing massive lacinial dentes and lacinial spurs. The latter are restricted closely to the terminal end of the lacinia.

The labium (Fig. 163) has an enormously expanded submentum; the palp is 3-jointed, and the glossae and paraglossae are distinct and well developed.

All the gills are concealed under a massive shield which consists of a backward prolongation of the mesothorax. The mesothoracic wing pad of the nymph has been included in this structure. This shield fits closely against the abdomen so as to form a special, highly developed gill chamber. The metathoracic wing pad is also concealed in this chamber. The gills are found on the first five abdominal segments, of which the first is a large foliaceous structure. The posterior four (Fig. 247) are also foliaceous but smaller and more elongated. On the inner margins of these, a number of dichotomously branched filaments arise.

Bœtisca seems a distinct entity in the phylogenetic arrangement of the mayflies. Its ancestral stock must have separated early from the remainder of the order. During its history certain parts have developed astonishing specializations, *e.g.*, the gill chamber, the anal area of the fore wing, the enormously expanded submentum, the distribution of the radius and of the anterior members of the Rs triad of the hind wing, and the peculiar penes. On the other hand, the behavior of the Cu veins of the fore wing, the forceps of the genitalia, the similar laciniae mobiles, and the highly modified but *single* gills are all primitive characters in the group.

SUMMARY

1. The mayfly venation is probably the most primitive in existence today and supports Lameere's wing vein hypothesis admirably.

2. The major veins that are to be found in the Ephemerida wings can be homologized vein for vein with those found in the primitive Dictyoneuridæ. None of the major veins have been lost as Lameere and Martynov have hypothesized.

3. The wings are of great importance in the study of the phylogeny of the group. The most primitive genus has a fore wing that tallies even to details with those of the fossil Protereismidæ. Those genera which have only one pair of wings, but that pair somewhat possessing the primitive ancestral shape, have arrived at that shape secondarily and not primarily.

4. The genitalia are of value as generic criteria in the nymphal state as well as in the adult state. Especially valuable are the forceps and the styliger plate. The primitive mayflies, during the adult period, probably had an undivided styliger plate and a 2-jointed forceps. The latter consisted of a long basal segment and a short terminal segment. The penes, while excellent as specific characters, are not good indices of generic relationship.

5. The maxillæ, mandibles, and labium can all be employed to advantage as phylogenetic indicators. The mandibles are more conservative than the other two. Usually the conditions found in the maxillæ are parallel to those of the labia.

6. The gills are highly diverse and are excellent indices of generic relationships. The ancestral mayfly nymphs had gills that consisted of simple tubular out-pushings. These have undergone many types of modification to arrive at the present day types.

7. *Siphlonurus* is the most primitive extant genus.

8. *Bœtisca* and *Cœnis* rose from the ancestral stock before *Siphlonurus*, but each has become highly specialized in its own peculiar manner.

9. The Baëtidae form one distinct phylogenetic stock, the origin of which can not be determined. It exhibits three separate paths of development within itself.

10. The Heptageniidae represent another branch of the phylogenetic tree. *Isonychia* occupies an inferior position, while the more highly specialized genera of the Heptageniidae can be divided into two sections.

11. *Ephemerella, Tricorythus, Blasturus, Choroterpes, Thraulus, Leptophlebia,* and the Ephemeridae constitute another great phylogenetic branch.

12. *Ephemerella* and *Tricorythus,* while very distinct now, arose together near the base of the last mentioned stock. Both *Ephemerella* and *Tricorythus* are highly specialized now, especially the latter. *Tricorythus* has no close relationship to *Caenis.*

13. *Blasturus, Choroterpes, Thraulus* and *Leptophlebia* are closely related and have retained many of the original characteristics of the stock from which they were derived.

14. *Potamanthus* stands intermediate between the remainder of the Ephemeridae and the Leptophlebiidae.

15. The remainder of the Ephemeridæ can, at this time, be divided into two main stocks: the first a closely knit one represented by *Hexagenia* and *Ephemera;* the second by *Polymitarcys* and *Pentagenia.* *Campsurus* can not be placed at present.

LITERATURE CITED

BANKS, N.

1910. Notes on our eastern species of the mayfly genus Heptagenia. Canad. Ent. 42: 197–202.

BENGTSSON, S.

1912. Neu Ephemeriden aus Schweden. Entomol. Tidskr. Stockholm. 33: 107–117.

1914. Bemerkungen uber die nordischen Arten der Gattung Cloëon Leach. Ent. Tidskr. 35: 210–220.

BÖRNER, C.

1908. Die Tracheenkiemen der Ephemeriden. Zool. Anz. 33: 806–823.

CALVERT, P.

1911. Studies on Costa Rican odonata. Ent. News 22: 49–65.

COMSTOCK, J. H.

1888. An introduction to entomology. Pp. 1–234.

COMSTOCK, J. H., and J. G. NEEDHAM.

1898. The wings of insects. Amer. Nat. 33: 117–126.

CRAMPTON, G. C.

1920. Remarks on the basic plan of the terminal abdominal appendages of the males of winged insects. Canad. Ent. 52: 178–184.

1921. The phylogenetic origin of the mandibles of insects and their arthropodan relatives. N. Y. Ent. Soc. 29: 63–97.

1922. A comparison of the first maxillae of apterygotan insects and crustacea from the standpoint of phylogeny. Ent. Soc. of Wash. 24: 65–84.

DRUCKEN, B.

1907. Die Tracheenkiemenmuskulatur der Ephemeriden unter Berücksichtigung der Morphologie des Insektenflügels. Zeit. fur Wissen. Zool. 87: 435–550.

EATON, A. E.

1883–87. A revisional monograph of recent Ephemeridae. London Trans. Linn. Soc. 3: 1–319.

GROS, A.

1923. Etudes sur les premiers stades des Ephemeres du Jura francais. Ann. Biol. Lacustre 12: 49–74.

HAGEN, H.

1889. Spaltung eines Flügels um das doppelte Adernetz zu zeigen. Zool. Anz. 12: 377–378.

HANDLIRSCH, A.
1906–08. Die Fossilen Insekten. Leipzig.

HEYMONS, R.
1896. Grundzuge der Entwicklung und der Korperbaues von Odonaten und Ephemeriden. Abhandl. der Kgl. preuss. Akademie d. Wissensch zu Berlin. 1896: 17–26. pl. 2.

IDE, F. P.
1930. Contribution to the biology of Ontario mayflies. Canad. Ent. 62: 204–213, 218–231.

KELLOGG, V. L.
1895. The Ephemeridae and venation nomenclature. Psyche 7: 311–315.

LAMEERE, A.
1917. Etude sur l'evolution des ephemeres. Bul. Soc. Zool. France 42: 41–59, 61–81.
1922. Sur la nervation aliare des insects. Bul. Class. des Sci. Acad. Roy. Belgique 1922: 38–149. (Translation in Psyche 30: 123–132.)

LESTAGE, J. A.
1917. Contribution a l'etude des larves des Ephemeres palearctiques. Ann. Biol. Lacustre 8: 213–456.
1918. Contribution a l'etude des larves des Ephemeres palearctiques. Ann. Biol. Lacustre 9: 79–182.

LUBBOCK, J.
1866. On the development of Chloen (Ephemera) dimiditum. Trans. Linn. Soc. 24: 61; 25: 477.

MCDUNNOUGH, J.
1924. New Canadian Ephemeridae with notes. Canad. Ent. 56: 113–133.
1925. Ephemeridae of Covey Hill. Trans. Roy Soc. Canada 19: 207–223.
1925. New Canadian Ephemeridae with notes. Canad. Ent. 57; 175.
1930. Ephemeroptera of the north shore of the Gulf of St. Lawrence. Canad. Ent. 62: 169–180.

MARTYNOV, A. V.
1922. The interpretation of the wing venation and tracheation of the Odonata and Agnatha. Rev. Russe Ent., 18(4): 145–174. (Translation in Psyche 37: 245–281.)

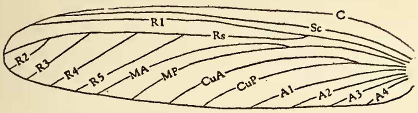
MORGAN, A. H.
1912. Homologies in the wing-veins of mayflies. Ann. Ent. Soc. of Am. 5: 89–106, 5 pl.
1913. A contribution to the biology of mayflies. Ann. Ent. Soc. of Am. 6: 371–401, 13 pl.

MURPHY, HELEN.
1922. Notes on the biology of some of our North American species of mayflies. Bul. 22 of the Lloyd Library.

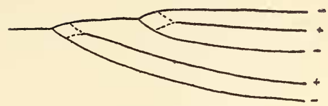
NEEDHAM, J. G.
1905. Mayflies and midges of New York. N. Y. State Mus. Bul. 86: 41–47.
1927. The Rocky Mountain species of the mayfly genus Ephemerella. Ann. Ent. Soc. of Am. 27: 107–117.
1927. A Baëtinae mayfly nymph with tusked mandibles. Canad. Ent. 59: 44–47.
NEEDHAM, J. G., and H. MURPHY.
1924. Neotropical mayflies. Lloyd Library, Bul. 24.
REDTENBACHER, J.
1886. Vergleichende Studien über das Flügelgeader der Insecten. Ann. des K. K. naturhistorischen Hofmuseums. Bd. 1, Heft 3: 153–231.
SELLARDS, E. H.
1907. Types of Permian insects: Part II, Plecoptera. Amer. Jour. Sci. 23: 345–355.
TILLYARD, R. J.
1922. The wing-venation of the order Plectoptera. Jour. Linn. Soc. London 35: 143–162.
1923. Descriptions of two new species of mayflies from New Zealand. Trans. N. Z. Inst. 54: 226–230.
1926. Insects of Australia and New Zealand. Sidney.
ULMER, G.
1920. Ubersicht über die Gattungen der Ephemeropteren nebst Bemerkungen über einzelne Arten. Stett. Ent. Zeit. 81: 97–144.
VAYASSIERE, A.
1882. Recherches sur l'organisation des Larves des Ephemerines. Ann. Sci. Nat. 13: 1–137.
WALKER, E. M.
1919. On the male and immature state of Grylloblatta compodeiformis Walk. Canad. Ent. 51: 131–146, 2 pl.
WALSH, B. D.
1862. List of the Pseudoneuroptera of Illinois. Proc. Acad. Nat. Sci. of Phil. 1862: 367–381.
WIEBE, A. H.
1926. The first three larval stages of Hexagenia bilineata Say. Ohio Jour. Sci. 26: 267–275, 1 pl.

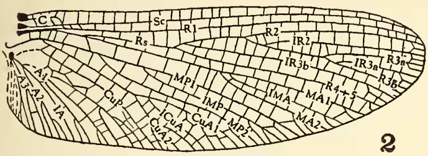
PLATE XVI

Figure 1. *Stenodictya Gaudryi* Brong. (After Handlirsch).
Figure 2. Hind wing of *Proteresma* sp? (After Tillyard.)
Figure 3. Fore wing of *Siphlonurus* sp?
Figure 4. Hind wing of *Siphlonurus* sp?
Figure 5. Fore wing of *Ecdyonurus* sp?—interpunctata complex.
Figure 6. Fore wing of *Ecdyonurus* sp?—tripunctata complex.
Figure 7. Hind wing of *Ecdyonurus* sp?—tripunctata complex.
Figure 8. Diagram of triadic system of branching of veins.
Figure 9. Hind wing of *Triblosoba.*
Figure 10. Fore wing of *Isonychia* sp?
Figure 11. Hind wing of *Isonychia* sp?
Figure 12. Fore wing of *Ecdyonurus* sp?
Figure 13. Fore wing of *Heptagenia* sp?—maculipennis complex.
Figure 14. Hind wing of *Heptagenia* sp?—maculipennis complex.

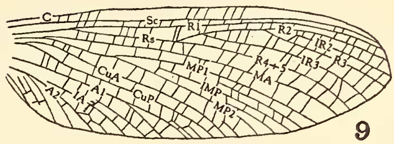


1

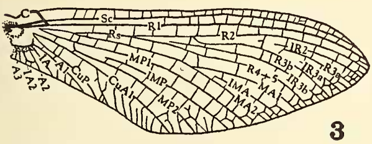

8



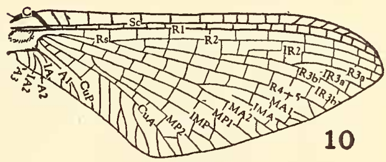
2



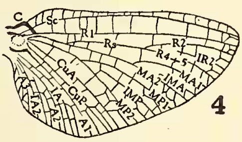
9



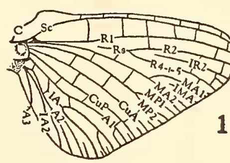
3



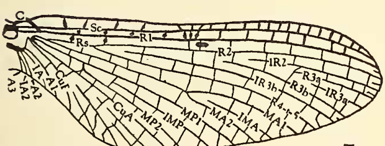
10



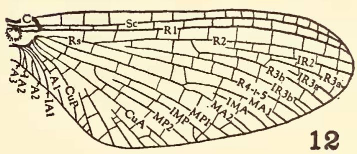
4



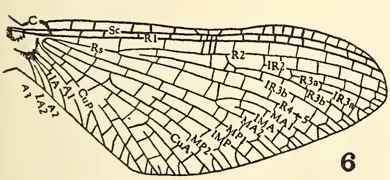
11



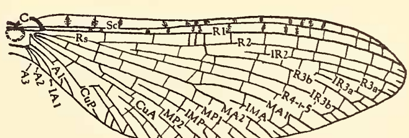
5



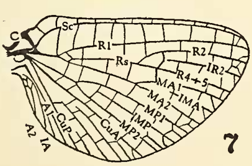
12



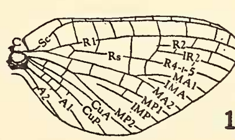
6



13



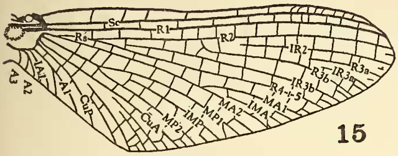
7



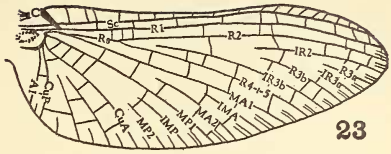
14

PLATE XVII

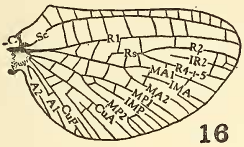
Figure 15. Fore wing of *Epeorus* sp?
Figure 16. Hind wing of *Epeorus* sp?
Figure 17. Fore wing of *Baëtis* sp.
Figure 18. Fore wing of *Pseudocloëon* sp?
Figure 19. Hind wing of *Baëtis* sp?
Figure 20. Hind wing of *Baëtis* sp?
Figure 21. Fore wing of *Leptophlebia* sp?
Figure 22. Hind wing of *Leptophlebia* sp?
Figure 23. Fore wing of *Callibaëtis* sp?
Figure 24. Hind wing of *Callibaëtis* sp?
Figure 25. Fore wing of *Centroptilium* sp?
Figure 26. Fore wing of *Cloëon* sp?
Figure 27. Hind wing of *Baëtis* sp?
Figure 28. Hind wing of *Centroptilium* sp?
Figure 29. Fore wing of *Thraulus* sp?
Figure 30. Hind wing of *Thraulus* sp?



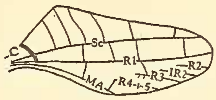
15



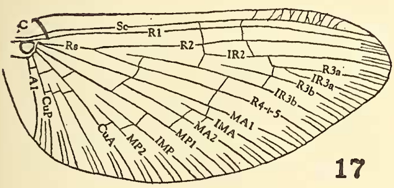
23



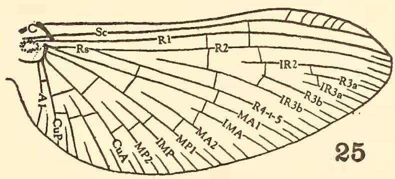
16



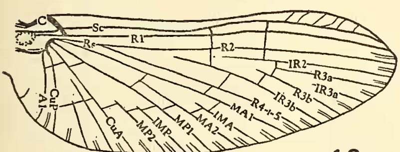
24



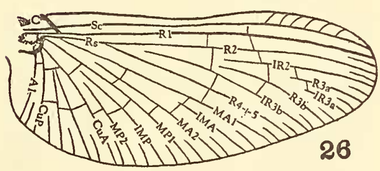
17



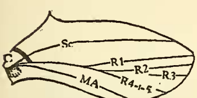
25



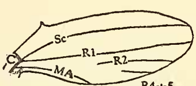
18



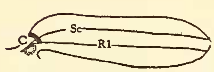
26



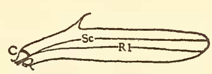
19



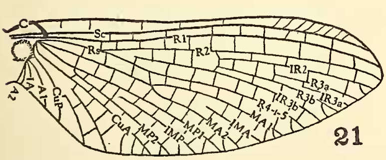
20



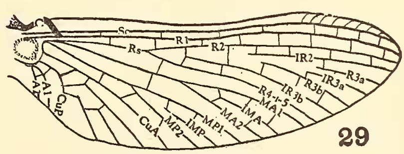
27



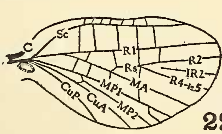
28



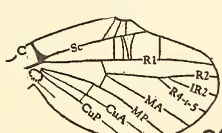
21



29



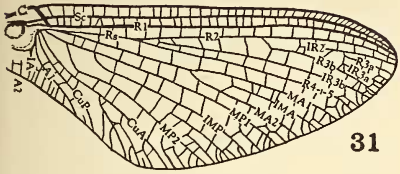
22



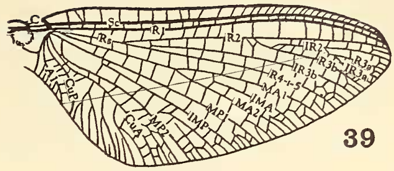
30

PLATE XVIII

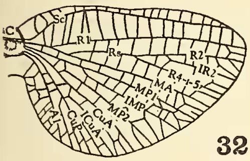
Figure 31. Fore wing of *Blasturus* sp?
Figure 32. Hind wing of *Blasturus* sp?
Figure 33. Hind wing of *Ephemera* sp?
Figure 34. Fore wing of *Potamanthus* sp?
Figure 35. Hind wing of *Potamanthus* sp?
Figure 36. Hind wing of *Pentagenia* sp?
Figure 37. Fore wing of *Pentagenia* sp?
Figure 38. Fore wing of *Campsurus* sp?
Figure 39. Fore wing of *Ephemera* sp?
Figure 40. Hind wing of *Hexagenia* sp?
Figure 41. Fore wing of *Hexagenia* sp?
Figure 42. Hind wing of *Polymitarcys* sp?
Figure 43. Fore wing of *Polymitarcys* sp?
Figure 44. Hind wing of *Campsurus* sp?



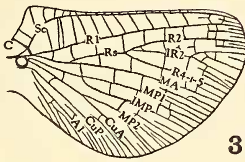
31



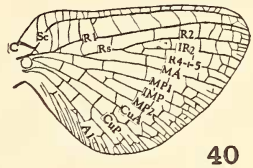
39



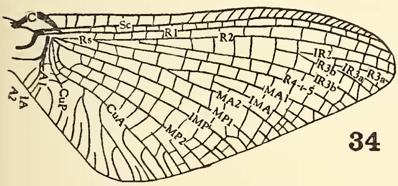
32



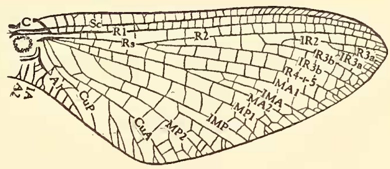
33



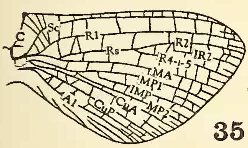
40



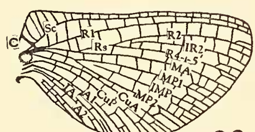
34



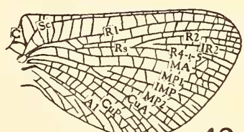
41



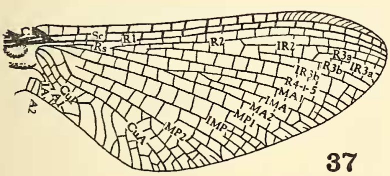
35



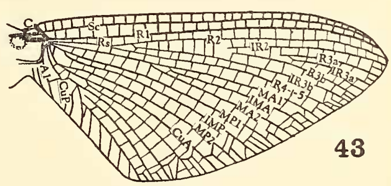
36



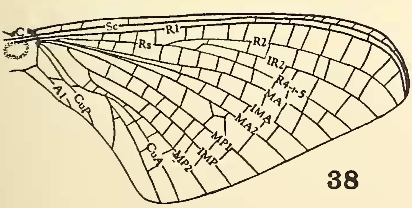
42



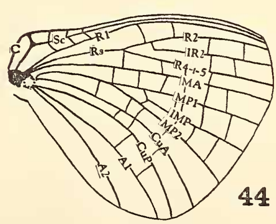
37



43



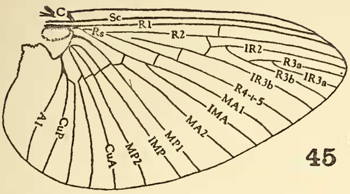
38



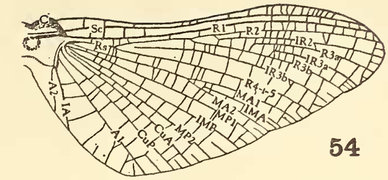
44

PLATE XIX

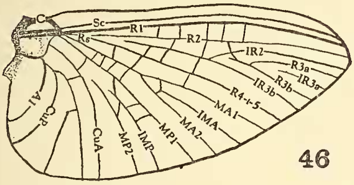
Figure 45. Fore wing of *Caenis* sp.
Figure 46. Fore wing of *Tricorythus* sp?
Figure 47. Hind wing of *Ephemerella* sp?
Figure 48. Genitalia of male imago, *Callibaëtis* sp?
Figure 49. Genitalia of male imago, *Heptagenia* sp?—maculipennis complex.
Figure 50. Genitalia of male nymph, *Heptagenia* sp?—maculipennis complex.
Figure 51. Genitalia of male nymph, *Ecdyonurus* sp?—interpunctata complex.
Figure 52. Genitalia of male nymph, *Ecdyonurus ithaca.* Need.
Figure 53. Genitalia of male imago, *Ecdyonurus* sp?
Figure 54. Fore wing of *Baëtisca* sp?
Figure 55. Fore wing of *Ephemerella* sp?
Figure 56. Genitalia of male nymph, *Callibaëtis* sp?
Figure 57. Genitalia of male nymph, *Isonychia* sp?
Figure 58. Genitalia of male nymph, *Siphlonurus* sp?
Figure 59. Genitalia of male imago, *Isonychia* sp?
Figure 60. Genitalia of male imago, *Ecdyonurus* sp?—interpunctata complex.
Figure 61. Genitalia of male imago, *Siphlonurus* sp?



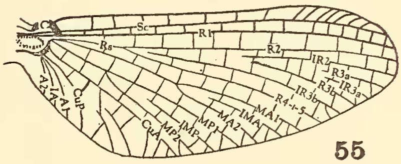
45



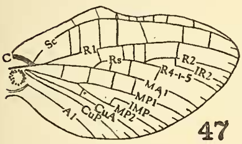
54



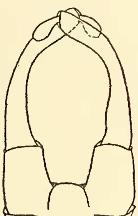
46

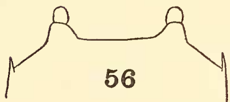


55

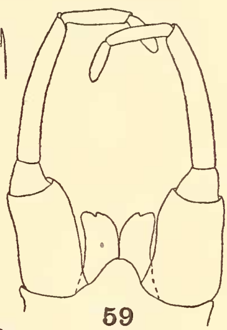


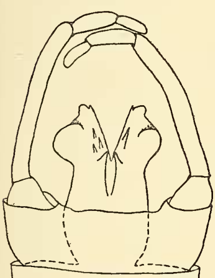
47

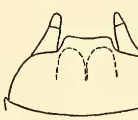

48

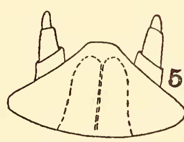

56


57


59

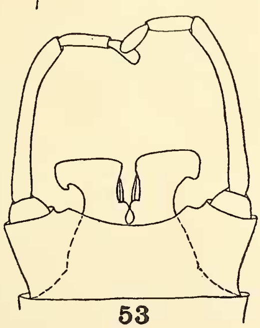

49

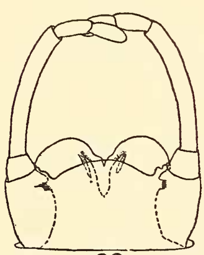

50


58


51


52


53


60

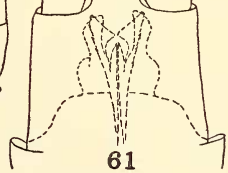

61

PLATE XX

Figure 62. Genitalia of male imago, *Heptagenia* sp?
Figure 63. Genitalia of male imago, *Thraulus* sp?
Figure 64. Genitalia of male imago, *Cloeon* sp?
Figure 65. Genitalia of male imago, *Baetis* sp?
Figure 66. Genitalia of male nymph, *Epeorus* sp?
Figure 67. Genitalia of male nymph, *Rithrogena* sp?
Figure 68. Genitalia of male imago, *Leptophlebia* sp?
Figure 69. Genitalia of male imago, *Centroptilium* sp?
Figure 70. Genitalia of male imago, *Pseudocloeon* sp?
Figure 71. Genitalia of male imago, *Ephemera* sp?
Figure 72. Genitalia of male imago, *Blasturus* sp?
Figure 73. Genitalia of male nymph, *Baëtis* sp?
Figure 74. Genitalia of male nymph, *Blasturus* sp?
Figure 75. Genitalia of male imago, *Baëtisca* sp?
Figure 76. Genitalia of male imago, *Hexagenia* sp?
Figure 77. Genitalia of male imago, *Potamanthus* sp?
Figure 78. Genitalia of male nymph, *Choroterpes* sp?
Figure 79. Genitalia of male nymph, *Potamanthus* sp?
Figure 80. Genitalia of male nymph, *Leptophlebia* sp?
Figure 81. Genitalia of male nymph, *Ephemera* sp?
Figure 82. Genitalia of male imago, *Pentagenia* sp?
Figure 83. Genitalia of male imago, *Polymitarcys* sp?
Figure 84. Genitalia of male imago, *Campsurus* sp?
Figure 85. Genitalia of male nymph, *Hexagenia* sp?
Figure 86. Genitalia of male nymph, *Polymitarcys* sp?

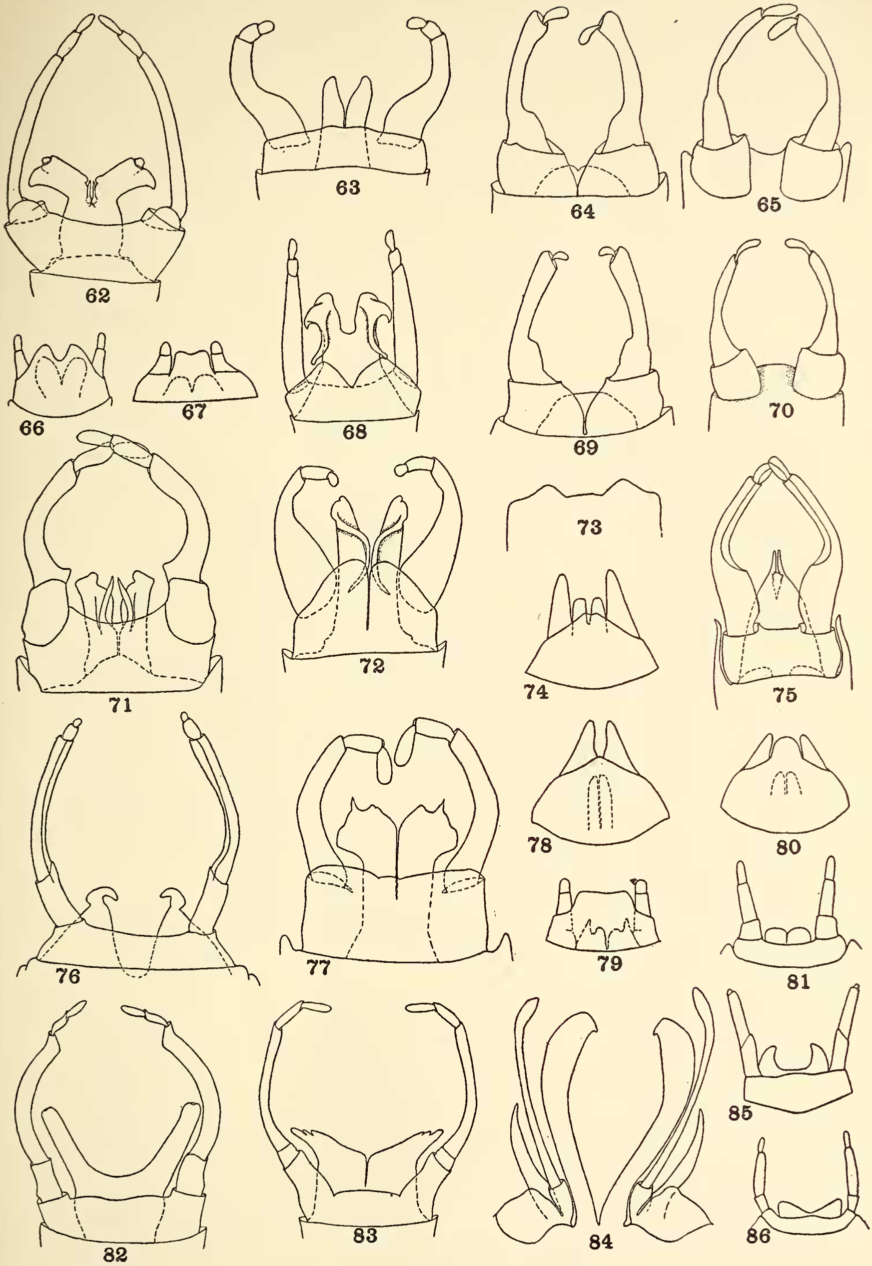

62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86

PLATE XXI

Figure 87. Genitalia of male imago, *Tricorythus* sp?
Figure 88. Genitalia of male imago, *Ephemerella* sp?
Figure 89. Genitalia of male imago, *Caenis* sp?
Figure 90. Genitalia of male nymph, *Caenis* sp?
Figure 91. Right mandible of nymph, *Isonychia* sp?
Figure 92. Genitalia of male nymph, *Ephemerella* sp?
Figure 93. Genitalia of male nymph, *Ephemerella* sp?
Figure 94. Genitalia of male nymph, *Tricorythus* sp?
Figure 95. Right mandible of nymph, *Siphlonurus* sp?
Figure 96. Right mandible of nymph, *Callibaëtis* sp?
Figure 97. Right mandible of nymph, *Ecdyonurus* sp?—interpunctata complex.
Figure 98. Right mandible of nymph, *Rithrogena* sp?
Figure 99. Right mandible of nymph, *Centroptilium* sp?
Figure 100. Right mandible of nymph, *Epeorus* sp?
Figure 101. Right mandible of nymph, *Heptagenia* sp?—maculipennis complex.
Figure 102. Right mandible of nymph, *Ecdyonurus* sp?

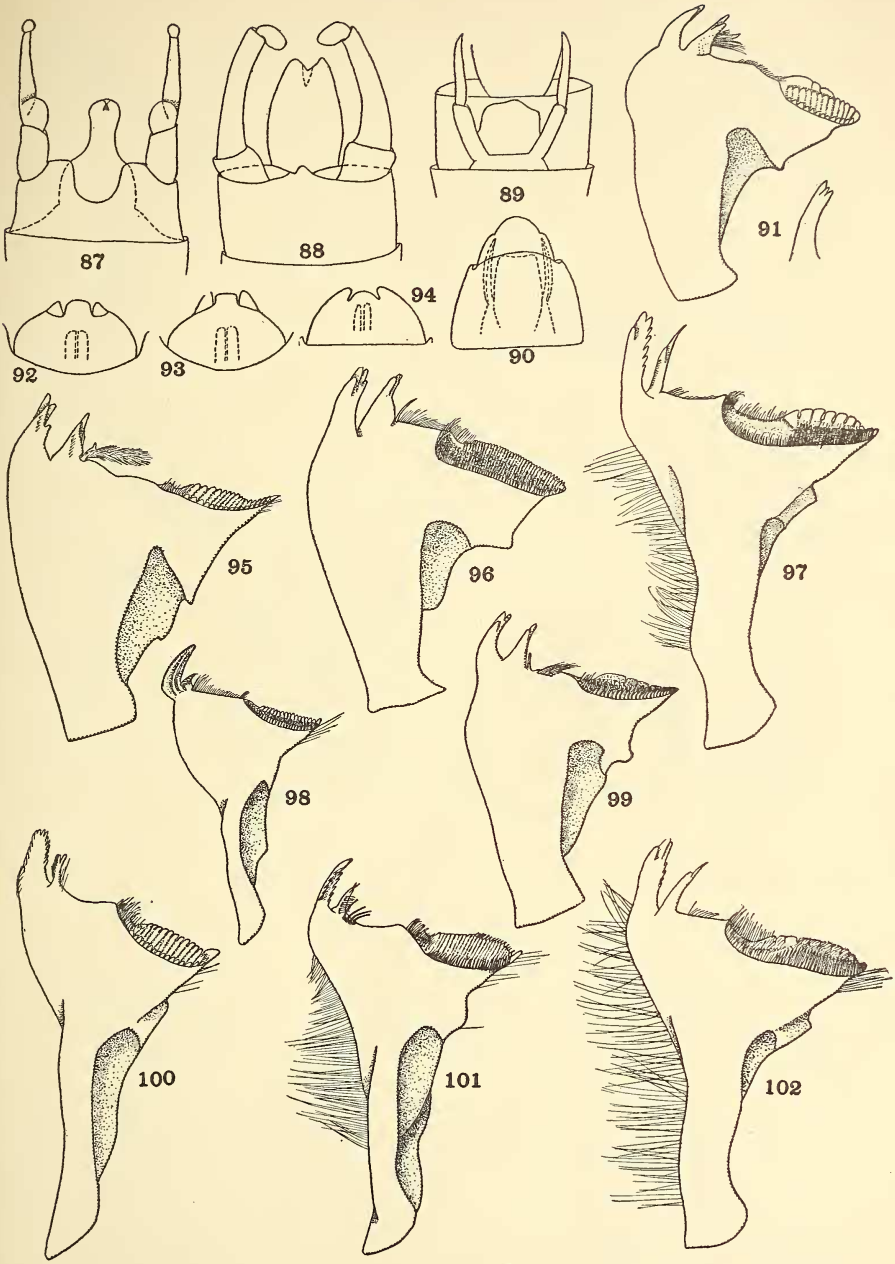

87
88
89
90
91
92
93
94
95
96
97
98
99
100
101
102

PLATE XXII

Figure 103. Right mandible of nymph, *Cloeon* sp?
Figure 104. Right mandible of nymph, *Potamanthus* sp?
Figure 105. Right mandible of nymph, *Hexagenia* sp?
Figure 106. Right mandible of nymph, *Polymitarcys* sp?
Figure 107. Right mandible of nymph, *Baëtis* sp?
Figure 108. Right mandible of nymph, *Potamanthus* sp?
Figure 109. Right mandible of nymph, *Ephemera* sp?
Figure 110. Right mandible of nymph, *Pentagenia* sp?
Figure 111. Right mandible of nymph, *Choroterpes* sp?
Figure 112. Right mandible of nymph, *Leptophlebia* sp?
Figure 113. Right mandible of nymph, *Ephemerella* sp?
Figure 114. Right mandible of nymph, *Tricorythus* sp?
Figure 115. Right mandible of nymph, *Blasturus* sp?

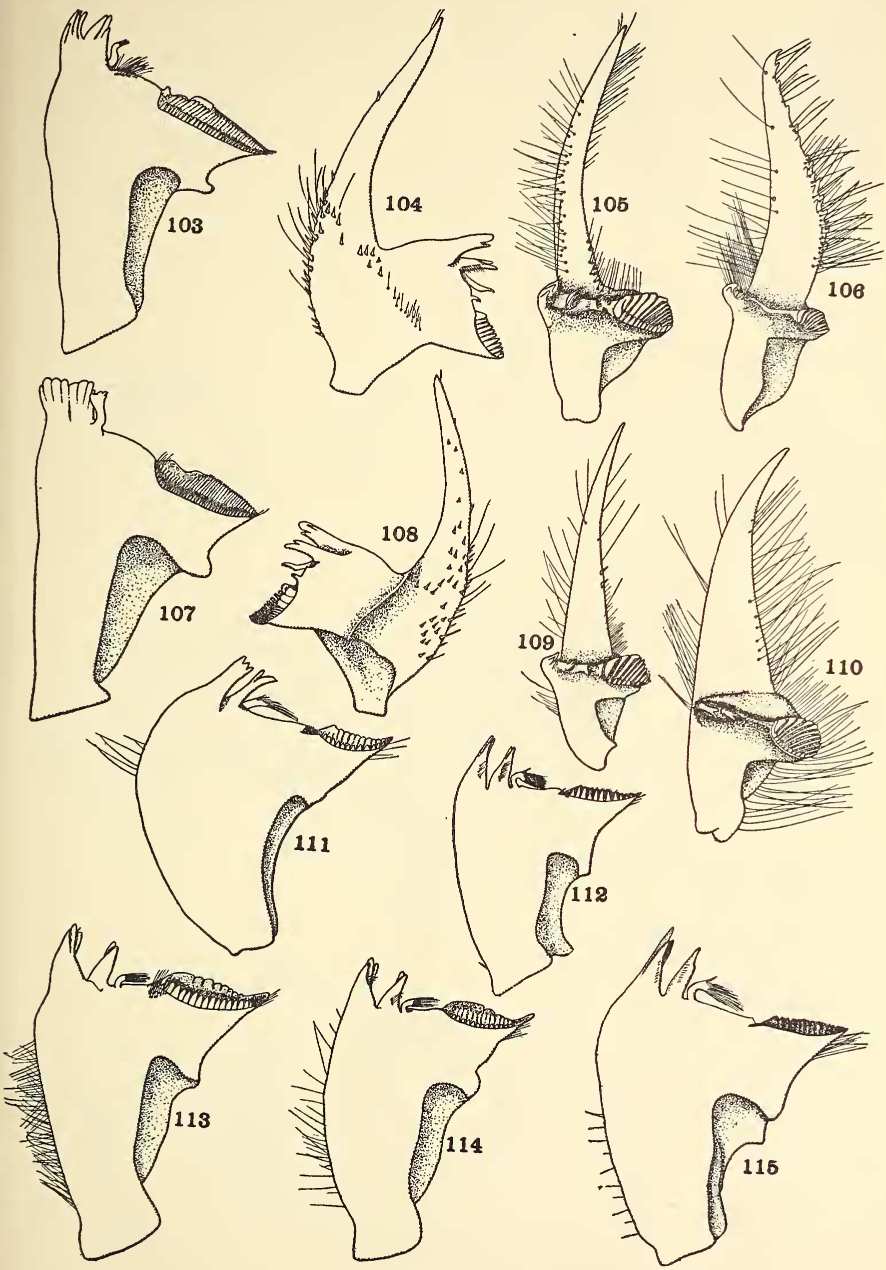

103
104
105
106
107
108
109
110
111
112
113
114
115

PLATE XXIII

Figure 116. Right mandible of nymph, *Baetisca* sp?
Figure 117. Right mandible of nymph, *Caenis* sp.
Figure 118. Maxilla of nymph, *Siphlonurus* sp?
Figure 119. Maxilla of nymph, *Isonychia* sp?
Figure 120. Maxilla of nymph, *Rithrogena* sp?
Figure 121. Maxilla of nymph, *Epeorus* sp?
Figure 122. Maxilla of nymph, *Centroptilium* sp?
Figure 123. Maxilla of nymph, *Callibaëtis* sp?
Figure 124. Maxilla of nymph, *Heptagenia* sp?—muculipennis complex.
Figure 125. Maxilla of nymph, *Ecdyonurus ithaca.* Need.
Figure 126. Maxilla of nymph, *Cloëon* sp?
Figure 127. Maxilla of nymph, *Baëtis* sp?
Figure 128. Maxilla of nymph, *Ecdyonurus* sp?—interpunctata complex.
Figure 129. Maxilla of nymph, *Blasturus* sp?
Figure 130. Maxilla of nymph, *Ecdyonurus* sp?

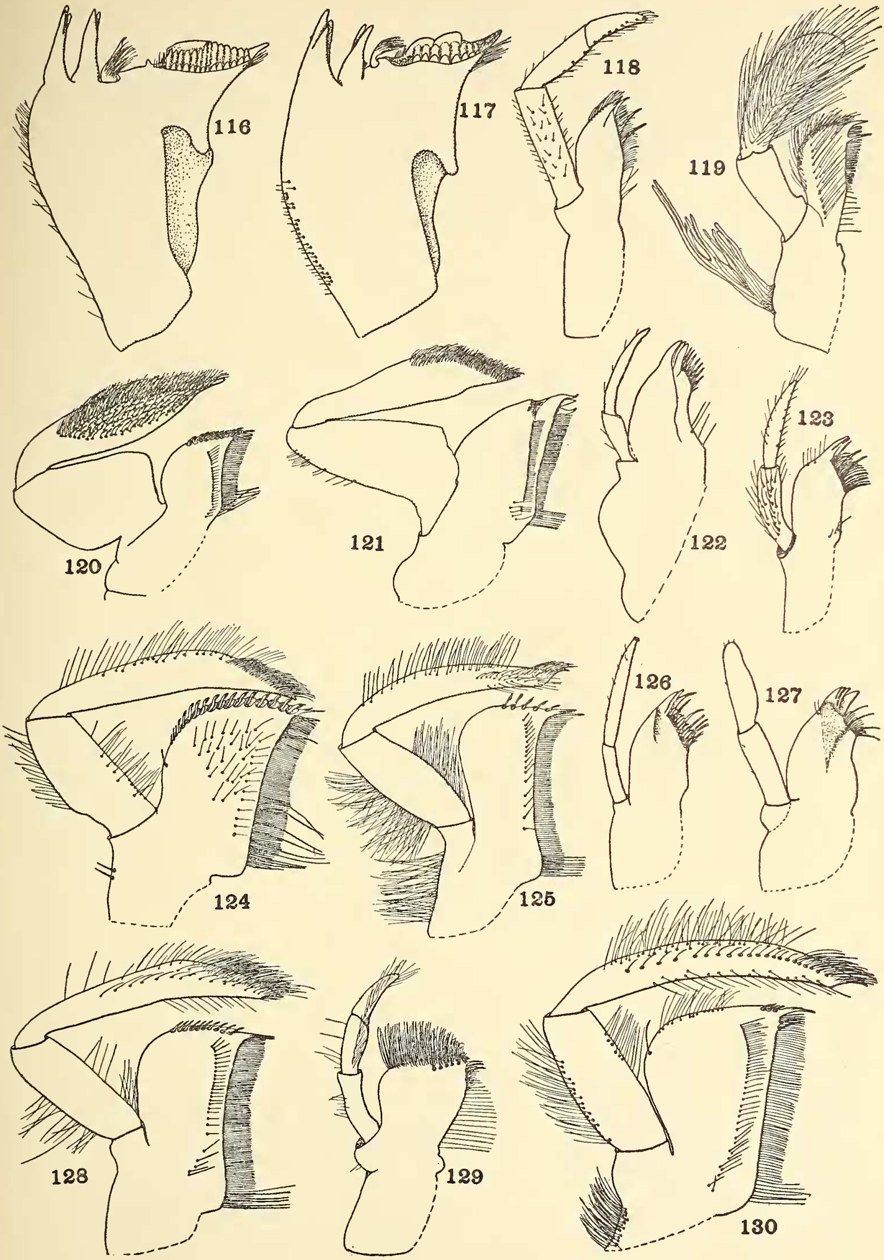

116
117
118
119
120
121
122
123
124
125
126
127
128
129
130

PLATE XXIV

Figure 131. Maxilla of nymph, *Choroterpes* sp?
Figure 132. Maxilla of nymph, *Leptophlebia* sp?
Figure 133. Maxilla of nymph, *Potamanthus* sp?
Figure 134. Maxilla of nymph, *Polymitarcys* sp?
Figure 135. Maxilla of nymph, *Ephemerella* sp?
Figure 136. Maxilla of nymph, *Ephemerella* sp?
Figure 137. Maxilla of nymph, *Tricorythus* sp?
Figure 138. Maxilla of nymph, *Hexagenia* sp?
Figure 139. Maxilla of nymph, *Ephemera* sp?
Figure 140. Maxilla of nymph, *Pentagenia* sp?
Figure 141. Maxilla of nymph, *Caenis* sp?
Figure 142. Labium of nymph, *Heptagenia* sp?—maculipennis complex.
Figure 143. Labium of nymph, *Siphlonurus* sp?
Figure 144. Maxilla of nymph, *Baetisca* sp?
Figure 145. Labium of nymph, *Ecdyonurus* sp?
Figure 146. Labium of nymph, *Epeorus* sp?
Figure 147. Labium of nymph, *Isonychia* sp?

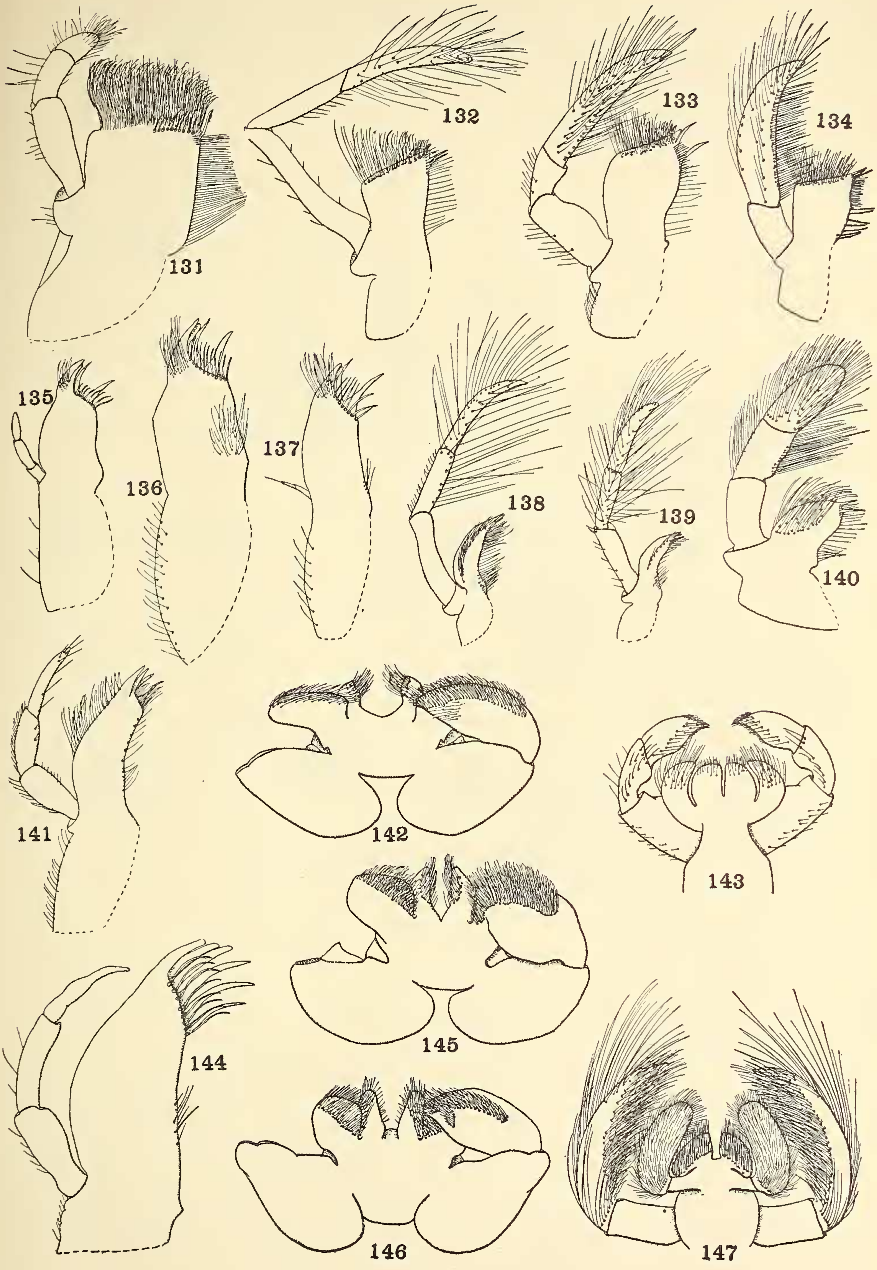

131
132
133
134
135
136
137
138
139
140
141
142
143
144
145
146
147

PLATE XXV

Figure 148. Labium of nymph, *Rithrogena* sp?
Figure 149. Labium of nymph, *Ecdyonurus ithaca.* Need.
Figure 150. Labium of nymph, *Centroptilium* sp?
Figure 151. Labium of nymph, *Blasturus* sp?
Figure 152. Labium of nymph, *Polymitarcys* sp?
Figure 153. Labium of nymph, *Ephemera* sp?
Figure 154. Labium of nymph, *Cloëon* sp?
Figure 155. Labium of nymph, *Choroterpes* sp?
Figure 156. Labium of nymph, *Pentagenia* sp?
Figure 157. Labium of nymph, *Callibaëtis* sp?
Figure 158. Labium of nymph, *Tricorythus* sp?
Figure 159. Labium of nymph, *Potamanthus* sp?
Figure 160. Labium of nymph, *Leptophlebia* sp?
Figure 161. Labium of nymph, *Hexagenia* sp?
Figure 162. Labium of nymph, *Baëtis* sp?
Figure 163. Labium of nymph, *Baetisca* sp?
Figure 164. Labium of nymph, *Ephemerella* sp?
Figure 165. Labium of nymph, *Ephemerella* sp?

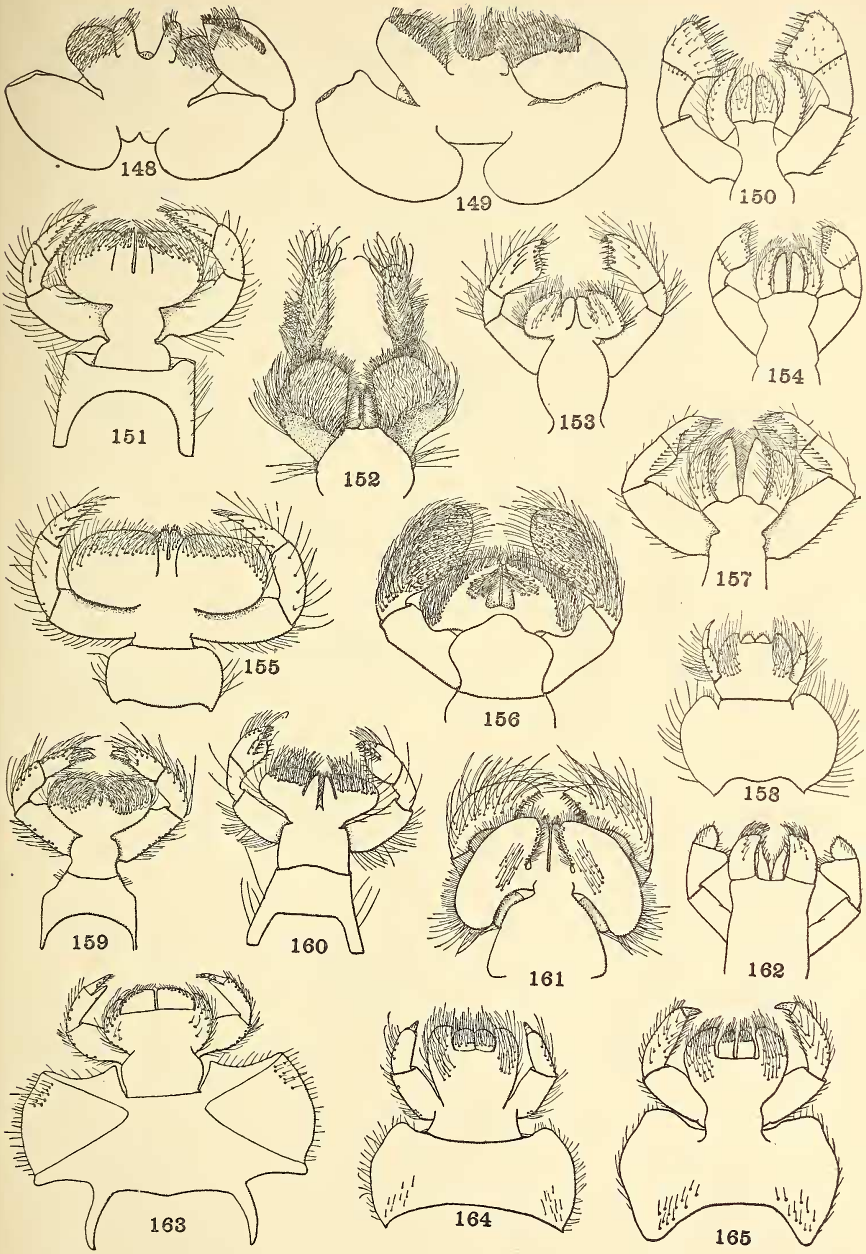

148
149
150
151
152
153
154
155
156
157
158
159
160
161
162
163
164
165

PLATE XXVI

Figure 166. Lacinia mobilis of nymph, *Siphlonurus* sp?
Figure 167. Lacinia mobilis of nymph, *Baetisca* sp?
Figure 168. Right lacinia mobilis of nymph, *Caenis* sp?
Figure 169. Left lacinia mobilis of nymph, *Caenis* sp?
Figure 170. Right lacinia mobilis of nymph, *Isonychia* sp?
Figure 171. Left lacinia mobilis of nymph, *Isonychia* sp?
Figure 172. Left lacinia mobilis of nymph, *Baëtis* sp?
Figure 173. Right lacinia mobilis of nymph, *Baëtis* sp?
Figure 174. Left lacinia mobilis of nymph, *Ecdyonurus* sp?
Figure 175. Right lacinia mobilis of nymph, *Blasturus* sp?
Figure 176. Left lacinia mobilis of nymph, *Blasturus* sp?
Figure 177. Right lacinia mobilis of nymph, *Leptophlebia* sp?
Figure 178. Left lacinia mobilis of nymph, *Leptophlebia* sp?
Figure 179. Left lacinia mobilis of nymph, *Callibaëtis* sp?
Figure 180. Right lacinia mobilis of nymph, *Callibaëtis* sp?
Figure 181. Right lacinia mobolis of nymph, *Choroterpes* sp?
Figure 182. Left lacinia mobilis of nymph, *Choroterpes* sp?
Figure 183. Right lacinia mobilis of nymph, *Centroptilium* sp?
Figure 184. Right lacinia mobilis of nymph, *Cloëon* sp?
Figure 185. Lacinia mobilis of nymph, *Heptagenia* sp?—maculipennis complex.
Figure 186. Right lacinia mobilis of nymph, *Potamanthus* sp?
Figure 187. Left lacinia mobilis of nymph, *Potamanthus* sp?
Figure 188. Right lacinia mobilis of nymph, *Ephemerella* sp?
Figure 189. Right lacinia mobilis of nymph, *Hexagenia* sp?
Figure 190. Left lacinia mobilis of nymph, *Hexagenia* sp?
Figure 191. Left lacinia mobilis of nymph, *Polymitarcys* sp?
Figure 192. Left lacinia mobilis of nymph, *Ephemerella* sp?
Figure 193. Right lacinia mobilis of nymph, *Ephemera* sp?
Figure 194. Left lacinia mobilis of nymph, *Ephemera* sp?
Figure 195. Left lacinia mobilis of nymph, *Pentagenia* sp?
Figure 196. Labium of nymph, *Caenis* sp?
Figure 197. Left lacinia mobilis of nymph, *Tricorythus* sp?

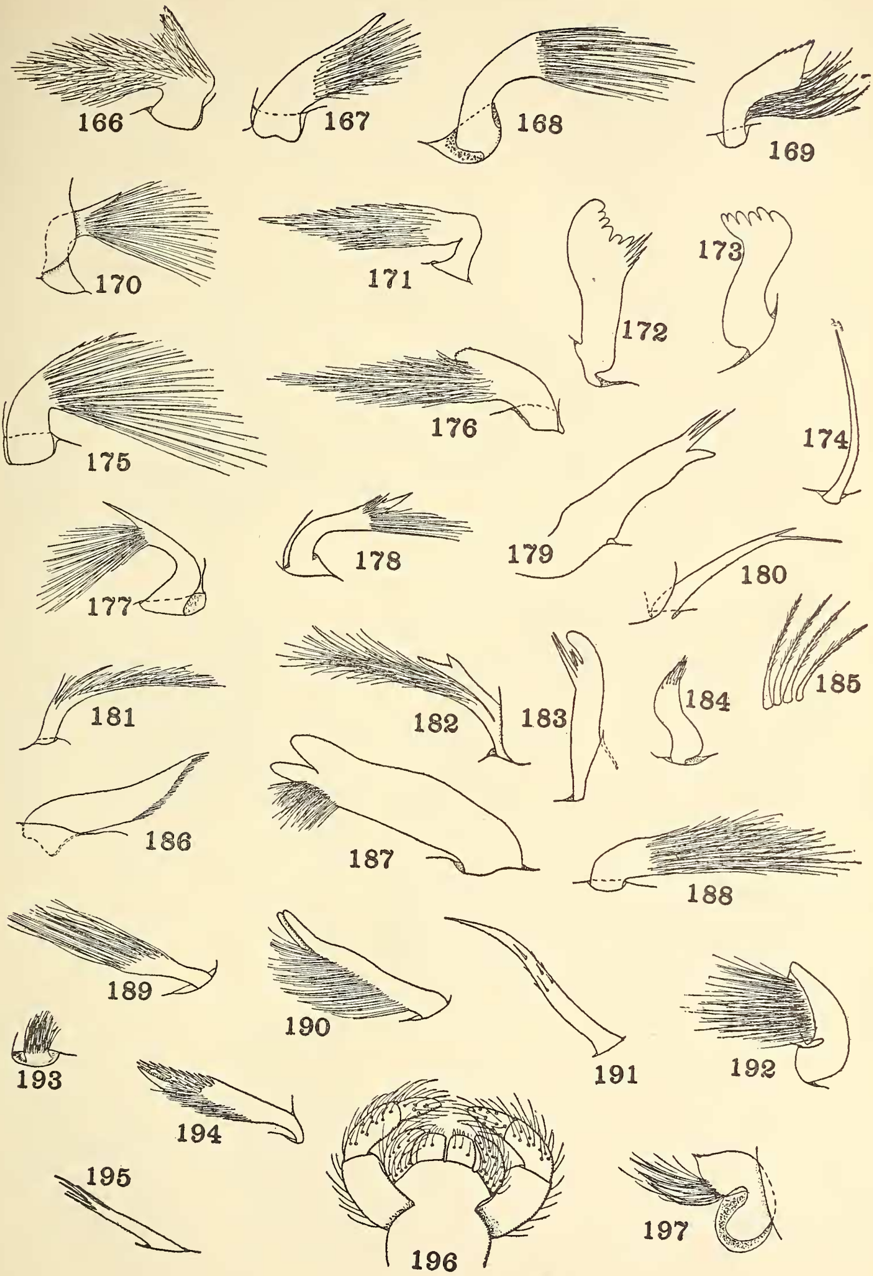

166
167
168
169
170
171
172
173
174
175
176
177
178
179
180
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195
196
197

PLATE XXVII

Figure 198. Anterior lamella of first gill of *Siphlonurus* sp?
Figure 199. Posterior lamella of first gill of *Siphlonurus* sp?
Figure 200. Posterior lamella of third gill of *Isonychia* sp?
Figure 201. Anterior lamella of third gill of *Ecdyonurus ithaca.* Need.
Figure 202. Posterior lamella of third gill of *Ecdyonurus ithaca.* Need.
Figure 203. Seventh gill of *Ecdyonurus ithaca.*
Figure 204. Seventh gill of *Siphlonurus* sp?
Figure 205. Anterior lamella of third gill of *Isonychia* sp?
Figure 206. Anterior lamella of third gill of *Ecdyonurus* sp?—interpunctata complex.
Figure 207. Posterior lamella of third gill of *Ecdyonurus* sp?—interpunctata complex.
Figure 208. Seventh gill of *Ecdyonurus* sp?—interpunctata complex.
Figure 209. Anterior lamella of third gill of *Epeorus* sp?
Figure 210. Posterior lamella of third gill of *Epeorus* sp?
Figure 211. Anterior lamella of third gill of *Heptagenia* sp?—maculipennis complex.
Figure 212. Seventh gill of *Cloëon* sp?
Figure 213. First gill of *Centroptilium* sp?
Figure 214. Third gill of *Cloëon* sp?
Figure 215. Seventh gill of *Heptagenia* sp?—maculipennis complex.
Figure 216. Posterior lamella of third gill of *Heptagenia* sp?—maculipennis complex.
Figure 217. Fourth gill of *Callibaëtis* sp?
Figure 218. Second gill of *Callibaëtis* sp?
Figure 219. Seventh gill of *Callibaëtis* sp?
Figure 220. Third gill of *Baetis* sp?
Figure 221. Third gill of *Centroptilium* sp?

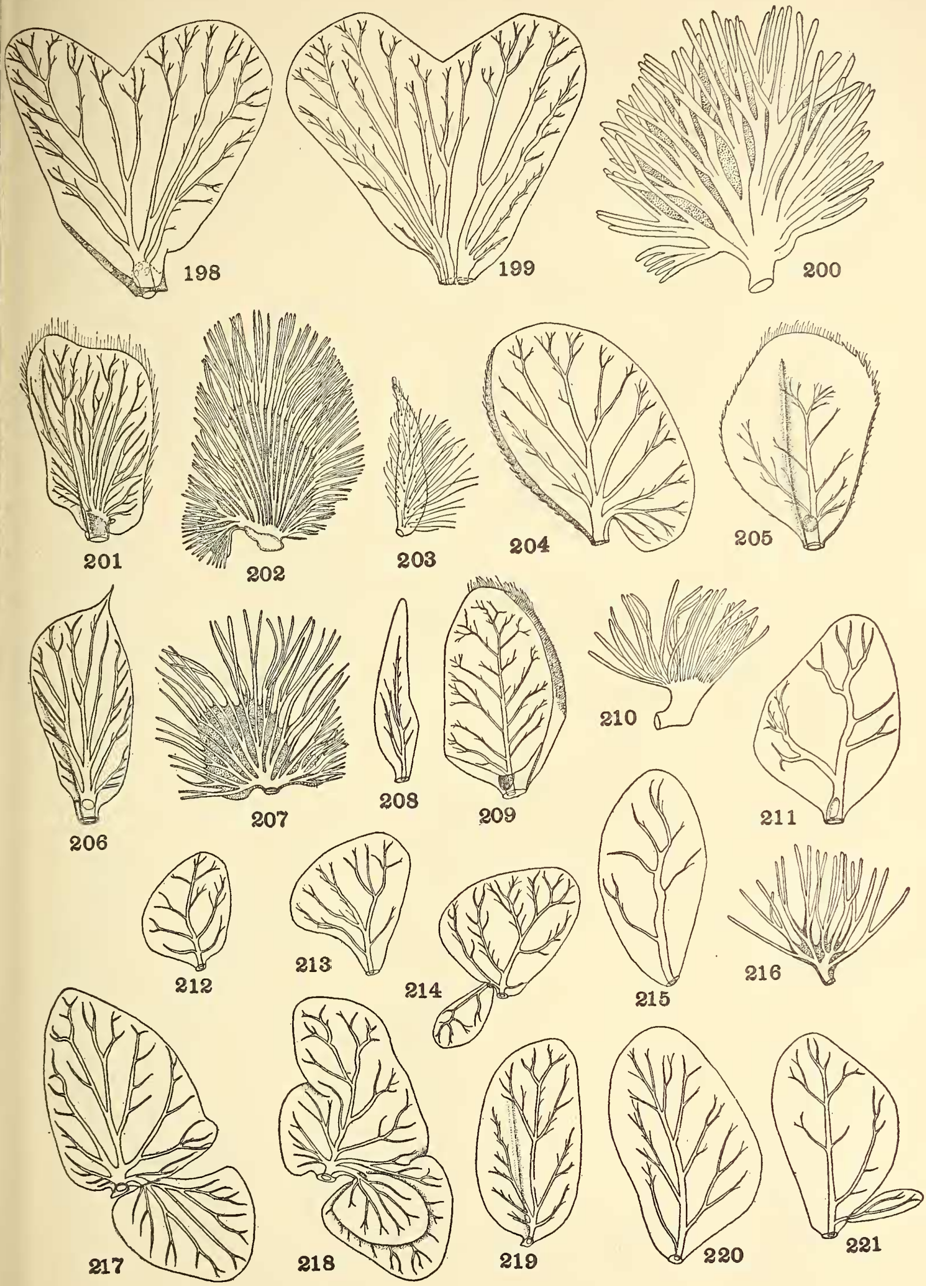

198
199
200
201
202
203
204
205
206
207
208
209
210
211
212
213
214
215
216
217
218
219
220
221

PLATE XXVIII

Figure 222. Anterior lamella of third gill of *Choroterpes* sp?
Figure 223. Posterior lamella of third gill of *Choroterpes* sp?
Figure 224. First gill of *Choroterpes* sp?
Figure 225. Anterior lamella of third gill of *Blasturus* sp?
Figure 226. Posterior lamella of third gill of *Blasturus* sp?
Figure 227. First gill of *Blasturus* sp?
Figure 228. Third gill of *Leptophlebia* sp?
Figure 229. Third gill of *Potamanthus* sp?
Figure 230. First gill of *Hexagenia* sp?
Figure 231. Posterior lamella of third gill of *Hexagenia* sp?
Figure 232. Anterior lamella of third gill of *Hexagenia* sp?
Figure 233. Anterior lamella of third gill of *Pentagenia* sp?
Figure 234. Posterior lamella of third gill of *Pentagenia* sp?
Figure 235. Seventh gill of twenty day old nymph of *Hexagenia* sp?
Figure 236. Sixth gill of eleven day old nymph of *Hexagenia* sp?
Figure 237. Posterior lamella of third gill of *Ephemerella* sp?
Figure 238. Third gill of *Ephemera* sp?
Figure 239. First gill of *Polymitarcys* sp?
Figure 240. Posterior lamella of seventh gill of *Ephemerella* sp?
Figure 241. Posterior lamella of third gill of *Tricorythus* sp?
Figure 242. Anterior lamella of third gill of *Ephemerella* sp?
Figure 243. Third gill of *Polymitarcys* sp?
Figure 244. First gill of *Ephemerella* sp?
Figure 245. Anterior lamella of second gill of *Tricorythus* sp?

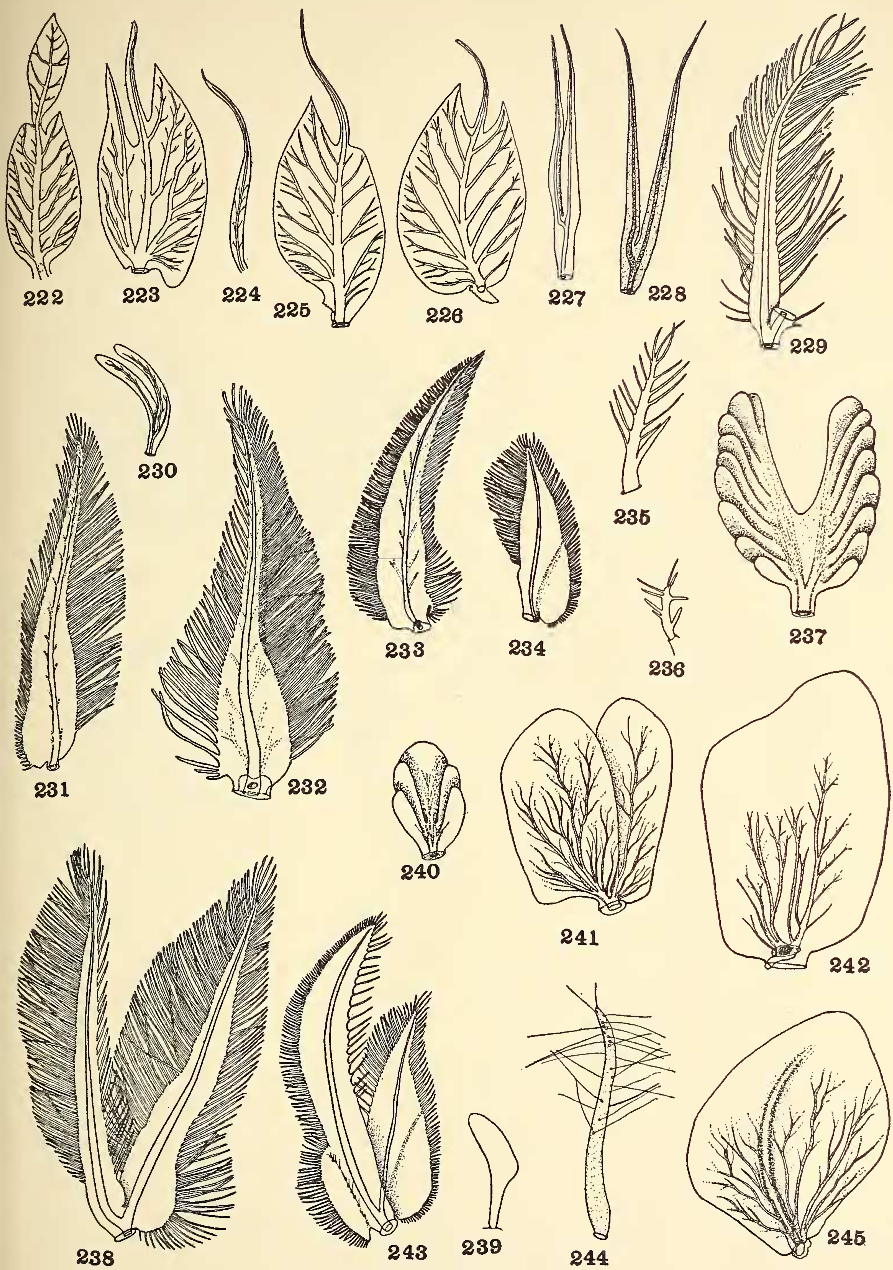
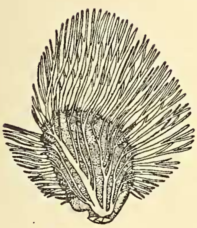
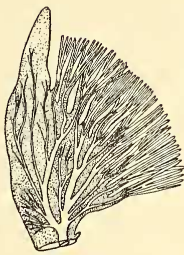
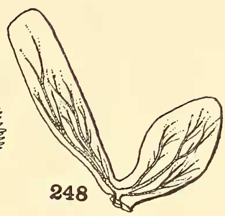

222
223
224
225
226
227
228
229
230
231
232
233
234
235
236
237
238
239
240
241
242
243
244
245

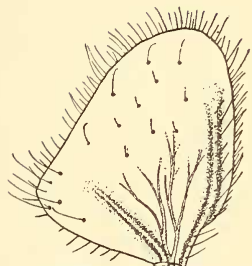
PLATE XXIX

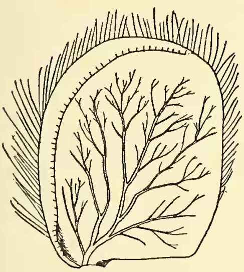
Figure 246. Third gill of *Caenis* sp?
Figure 247. Second gill of *Baetisca* sp?
Figure 248. Posterior lamella of first gill of *Tricorythus* sp?
Figure 249. Anterior lamella of first gill of *Tricorythus* sp?
Figure 250. Second gill of *Caenis* sp?
Figure 251. First gill of *Caenis* sp?


246


247


248


249


250


251